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Seattle, Washington

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PHASE DIFFERENCE BETWEEN CALCIFICATION AND ORGANIC MATRIX FORMATION IN THE DIURNAL GROWTH OF OTOLITHS IN THE RAINBOW TROUT, *SALMO GAIRDNERI*

YASUO MUGIYA[1]

ABSTRACT

The relative role of calcium and organic matrix deposition in the formation of daily increments in otoliths was studied in in vitro preparations of otolith-containing sacculi of rainbow trout, *Salmo gairdneri*. Sacculi were incubated in a Ringer solution containing both ^{45}Ca and ^{3}H-glutamic acid for 2 hours at 6-h intervals throughout a 24-h period and then the uptake of these isotopes was determined for both otolith and saccular tissue fractions. Serum calcium and sodium concentrations were also analyzed for diurnal variations.

Serum calcium concentrations varied diurnally by 8% in a single phasic pattern, reaching a peak at dusk (1600 h) and a nadir at night (2200 h), while sodium concentrations remained almost constant throughout a 24-h period. Diurnal variation in the otolith's uptake of calcium and glutamic acid showed discrete, antiphasic cycles. The rate of calcium uptake varied in a pattern closely resembling that of serum calcium (the peak at 1600 h and the nadir at 2200 h); glutamic acid uptake remained almost constant during the daytime and peaked at night (2200 h). The results indicate that in rainbow trout daily increments of otoliths are formed by the antiphasic deposition of calcium and organic matrix.

Teleost otoliths consists of calcium carbonate in aragonite form and an organic matrix in which acidic amino acids dominate (Degens et al. 1969). Concentric rings within the microstructure of otoliths are commonly laid down on a daily basis (Campana and Neilson 1985; Jones 1986). A unit increment comprises one light and one dark ring when observed under transmitted light. These bipartite structures are also observable by scanning electron microscopy. After etching with weak acids or decalcification with calcium-chelating agents, they usually appear as an alternating pattern of well-calcified zones with elongated crystals perpendicular to the otolith periphery (accretion zone) and narrow grooves which intersects the crystal development at right angles (discontinuous zone). However, some recent studies (Mugiya and Muramatsu 1982; Watabe et al. 1982; Takahashi 1982; Morales-Nin 1987) showed that if the etching and subsequent treatments were carried out carefully, the organic matrix could be preserved in the discontinuous zone, appearing as a raised ridge. After complete decalcification of the otolith, Dean et al. (1983) and Radtke and Targett (1984) observed incremental features in the remaining matrix. Thus, stated in relative terms, the accretion and discontinuous zones appear to be alternatively calcium-dominant and matrix-dominant structures. However, Watabe et al. (1982) observed that morphologically similar matrix material extended continuously between accretion and discontinuous zones, and proposed a possible mechanism for otolith increment formation. For their recently proposed model, Campana and Neilson (1985) also assumed continuous matrix formation in diurnal otolith growth.

Based on these morphological studies, three hypotheses might account for the formation of the bipartite structure of otolith increments: 1) both organic matrix and calcium deposition show diurnal variations occurring in antiphase, 2) calcium deposition varies diurnally, while matrix deposition does not, and 3) calcium deposits at a constant rate throughout a 24-h period, while matrix deposition varies diurnally. All these would result in the formation of alternate zones where calcium or matrix deposition predominated. Of these, the last possibility can be excluded. Physiological studies indicate that the rate of calcium uptake by otoliths varies diurnally in goldfish and rainbow trout (Mugiya et al. 1981; Mugiya 1984).

The present study was undertaken to investigate diurnal variation in matrix formation and to

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relate its phase, if apparent, to otolith calcification. Because diurnal variations in otolith calcification show seasonality (Mugiya 1984), an ideal way to examine such a phase relationship is to determine the rates of calcium and matrix deposition on a single otolith simultaneously, using a double-tracer method and in vitro, isolated sacculi from rainbow trout. Diurnal profiles of glutamic acid and calcium uptake were examined in the otoliths and the remaining saccular tissue. Serum calcium and sodium concentrations were also measured for diurnal variations.

MATERIALS AND METHODS

Rainbow trout, *Salmo gairdneri*, 29-31 cm in standard length, were obtained from a commercial dealer and reared in a pair of outside ponds supplied with 14°C running water. They were fed trout food pellets once a day at around 0845 h. Two females showed maturing ovaries, so their data were omitted. No males were excluded because maturing testes have little, if any, effect on the level of serum calcium. The experiment was carried out in December 1984. Dusk occurred at 1600 h and dawn at 0700 h.

At each sampling time, five or six fish were gently netted one at a time. Blood was immediately collected from the caudal vessels by cutting the tail of the fish and draining it into test tubes. After centrifugation, the separated sera were stored at −30°C for 6-24 hours and analyzed for calcium and sodium concentrations by flame photometry using an atomic absorption spectrophotometer (Hitachi[2] 518).

After blood collection, the head was severed, trimmed, and placed in an oxygenated Ringer solution kept at 14°C. The sacculi were dissected under a binocular microscope according to a previously described technique (Mugiya 1984). The pair of sacculi were placed in the incubation medium, and the next fish was netted. Time was recorded to ensure that sacculi from each fish were incubated for the same length of time.

Isolated sacculi were placed in a glass vessel and incubated in 50 mL of a Ringer solution (Mugiya 1986) containing ^{45}Ca and ^{3}H-glutamic acid (New England Nuclear) at concentrations of approximately 0.17 μCi/mL and 0.33 μCi/mL respectively. The incubation was carried out with oxygenation at 14°C for 2 hours. To determine proper incubation times, the uptake of ^{3}H-glutamic acid by otoliths was plotted against time; although in this preliminary experiment, sacculi were incubated for periods of up to 3 hours, steady-state levels were obtained in less than 2 hours.

After incubation, sacculi were rinsed several times in the radioisotope-free Ringer solution and separated into otolith and saccular tissue fractions under a binocular microscope. The separated otoliths were lightly rinsed in water, placed in individual counting vials, dried at 90°C overnight and then weighed. The saccular tissue was directly placed in the vial without a further rinse and air-dried. These samples were solubilized in a mixture of 0.2 mL perchloric acid and 0.2 mL hydrogen peroxide at about 80°C for 2 hours, and added to Scintisol EX-H (Wako) for counting (liquid scintillation spectrometer, Aloka LSC-673).

Tritium and ^{45}Ca activities were measured simultaneously using two channels with narrowed windows, 50-300 for ^{3}H and 70-900 for ^{45}Ca. Although the amount of ^{3}H activity entering the Ca channel was found to be practically negligible, ^{45}Ca would certainly affect counts on the H channel, despite the window conditions. Therefore, counts on the H channel were corrected by the equation:

$$^{3}H \text{ activity} = H - 1/\alpha \, Ca \qquad (1)$$

where H and Ca represent counts on the H and Ca channels respectively, and α (contamination ratio) is experimentally defined as $\log \alpha = 0.1386R - 0.0488$ where R is a ratio determined for the quenching level of each sample. The validity of this correction was further checked by another equation based on differences in the physical half-life of the isotopes:

$$^{3}H \text{ activity} = \frac{Ca_0H_2 - Ca_2H_0}{Ca_0 - Ca_2} \qquad (2)$$

where H_0 and Ca_0 are counts on the H and Ca channels at time 0 respectively, and H_2 and Ca_2 are those recounted a few months later. Because these two methods of discrimination gave essentially the same results, the data from Equation (1) were presented in this study.

Some rainbow trout have an aberrant otolith in either or both of their sacculi (Mugiya 1972). If

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

the highly aberrant form was found by inspection after incubation, it was excluded from the data.

RESULTS

Serum calcium concentrations varied diurnally by approximately 8% in a single phasic pattern (Fig. 1). The maximum level (5.47 meq/L) occurred at dusk (1600 h), followed by a rapid decrease ($P < 0.05$) to a nadir (5.04 meq/L) at night (2200 h). The level then gradually increased toward the next peak. In contrast, serum sodium concentrations showed a statistically insignificant variation of only 0.6% ($P > 0.05$; 148.1-149.0 meq/L) throughout a 24-h period.

When otolith-containing sacculi were incubated with ^{3}H-glutamic acid, the saccular tissue (without otoliths) was almost saturated with the isotope within the first 30 minutes or hour of incubation (Fig. 2). Otoliths also showed a considerable uptake (about 60% of the total) of the isotope in the first 30 minutes, followed by a gradual increase in radioactivity until 3 hours, when the incubation was terminated. Tritium activities were always 6-8 times higher in the saccular tissue than in the respective otolith (Fig. 2). The time-related uptake of ^{45}Ca by these tissue fractions has been reported (Mugiya 1984). In that study, the saccular tissue was saturated with ^{45}Ca within the first hour of incubation, while otoliths showed an almost linear increase in ^{45}Ca uptake during the first 5 hours at which point the incubation was terminated.

The uptake of calcium by otoliths varied diurnally (Fig. 3), and the pattern was quite similar to that of diurnal variations in serum calcium concentrations (Fig. 1). The rate of calcium uptake was intermediate at 1000 h, peaked at dusk (1600 h), and then decreased significantly ($P < 0.02$) by 37% to a nadir at night (2200 h). The low rate persisted through the night, increasing slightly at 0400 h. Clearly otolith calcification proceeded more actively during the daytime. The uptake of glutamic acid by the same otoliths also showed a diurnal variation, and its profile was almost antiphasic to that of calcium uptake (Fig. 3). The rate of the uptake remained rather low during the daytime with a small nadir at dusk (1600 h). Then the rate increased significantly ($P < 0.05$) to a peak at night (2200 h), followed by a return to the daytime level. Thus the most active deposition of otolith matrix (at least proteins) occurred during the first half of the nighttime period, when calcium deposition was at its lowest level.

The uptake of glumatic acid by the saccular tissue showed significant ($P < 0.02$), diurnal

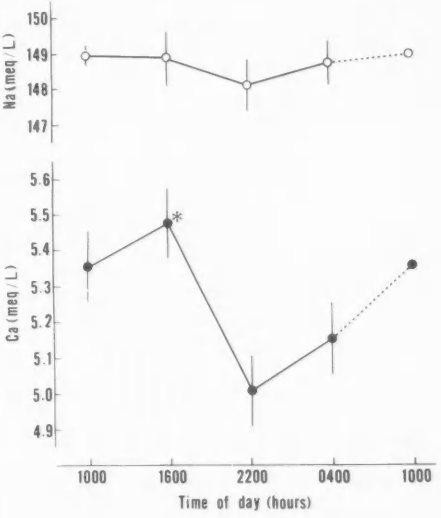

FIGURE 1.—Diurnal variations in serum calcium (●) and sodium (○) concentrations in rainbow trout. Each plotted value represents mean ± SE of 5 or 6 fish. *$P < 0.05$ for 2200 h.

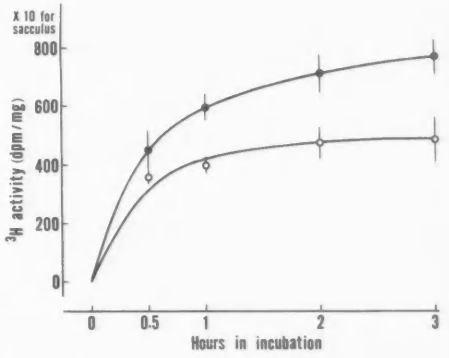

FIGURE 2.—Time course for the in vitro uptake of ^{3}H-glutamic acid by otoliths (●) and the saccular tissue (○) of isolated sacculi in rainbow trout. The radioactivity of the saccular tissue is expressed as dpm per otolith weight (mg) because the dry weight of the individual saccular tissue was too light to be determined accurately. Each plotted value represents mean ± SE of 8-10 samples.

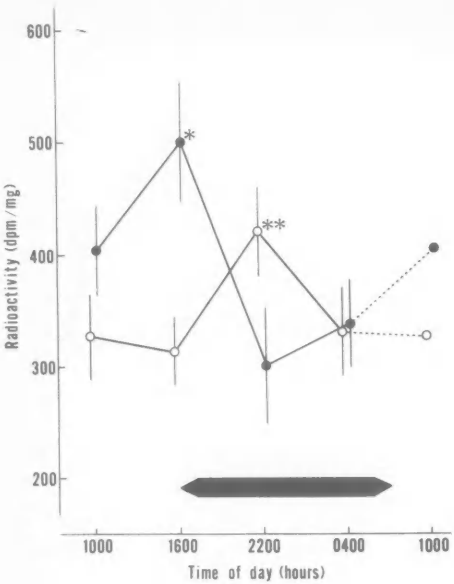

FIGURE 3.—Diurnal variations in the in vitro uptake of ^{45}Ca (●) and ^{3}H-glutamic acid (○) by otoliths in rainbow trout. Each plotted value represents mean ± SE of 8-10 samples. Dark horizontal bar indicates nocturnal and twilight periods. $*P < 0.02$ for 2200 h; $**P < 0.05$ for 1600 h.

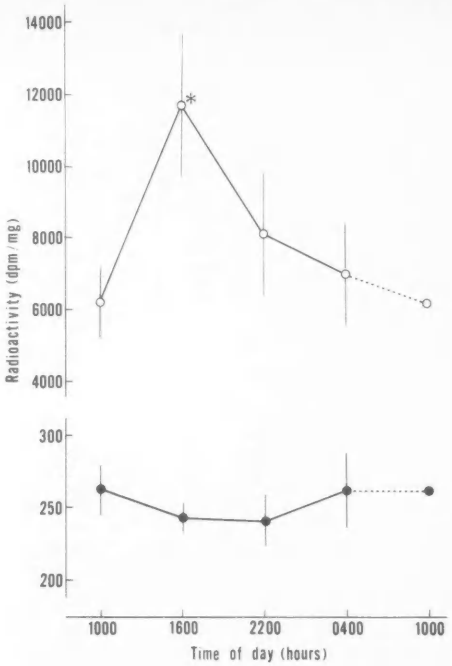

FIGURE 4.—Diurnal variations in the in vitro uptake of ^{45}Ca (●) and ^{3}H-glutamic acid (○) of saccular tissue in rainbow trout. Each plotted value represents mean ± SE of 8-10 samples. $*P < 0.02$ for 1000 h.

variation with a single peak at 1600 h when matrix deposition on the otoliths was lowest (Fig. 4). Note that the active biosynthesis of matrix proteins in the saccular tissue is not necessarily followed by their instantaneous deposition on the otoliths, suggesting the presence of cyclic secretion activity in the cells of the sacculus. The rate of calcium uptake by the saccular tissue did not vary much throughout a 24-h period (Fig. 4).

Ratios of counts of ^{45}Ca and ^{3}H-glutamic acid in the respective otoliths magnified the antiphasic relationship between ^{45}Ca and ^{3}H uptake (Fig. 5). Significant variation ($P < 0.01$) between the peak (1600 h) and the nadir (2200 h) demonstrates the much greater deposition of calcium relative to glutamic acid during the daytime, which suggests that in December the accretion zone forms during the daytime with its peak at dusk.

DISCUSSION

Although previous studies (Mugiya et al. 1981; Mugiya 1984) showed that otoliths grew by the diurnal deposition of calcium, it remained to be determined whether matrix deposition on the otoliths was diurnal or not. Histochemically, otolith matrix consists of various kinds of substances such as proteins, acid mucopolysaccharides, PAS-positive materials, and lipids (Mugiya 1968). Of these, proteins are the most dominant component and are characterized by a high content of acidic amino acids (Degens et al. 1969). In the present study the diurnal deposition of otolith matrix was evident when examined in terms of the incorporation of glutamic acid into otoliths, showing a single peak at night. Interestingly, calcium deposition on the same otoliths proceeded most actively at dusk, followed by minimum deposition at night. Thus, it is concluded, in rainbow trout kept under natural photoperiod, the pace of otolith calcification is almost antiphasal to the pace of matrix deposition on the otoliths.

The present results, where both calcium and

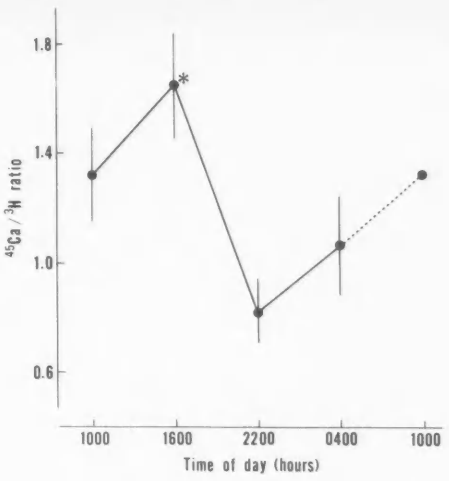

FIGURE 5.—Diurnal change in the ratio of ^{45}Ca to ^{3}H-glutamic acid activity incorporated into the same otoliths in rainbow trout. Each plotted value represents mean ± SE of 8-10 samples. $^{*}P < 0.01$ for 2200 h.

matrix deposition on otoliths varied diurnally in antiphase, indicate the relative importance of these substances for daily increment formation in otoliths. The accretion zone is formed predominantly by calcium deposition, while the discontinuous zone results from reduced calcium and substantially increased matrix deposition on the otoliths. These findings coincide with the morphological observation that the accretion zone is a crystalline layer with organic materials and the discontinuous zone is a layer containing more organic materials and less calcium (Mugiya and Muramatsu 1982; Watabe et al. 1982). Watabe et al. (1982) observed that the matrix fibers and their aggregates were morphologically similar in the two zones and continuous throughout in *Tilapia* and *Fundulus* otoliths. Based on these observations, they have suggested that the matrix materials are identical in the zones and their deposition might be an uninterrupted event during diurnal otolith growth. They also stated that this did not necessarily imply that the rate of organic matrix secretion was diurnally constant. In fact, the present study reveals that diurnal variations in the rate of the matrix deposition, coupled with variations in calcium deposition, play an important role in otolith increment formation.

Although the sacculus contains the otolith, otolithic membrane, and endolymph, a high content of acidic amino acids is characteristic of the calcified otolith (Degens et al. 1969). Therefore, variations in the uptake of glutamic acid by the saccular tissue should be closely related to the activity of the matrix formation of the otolith, even though glutamate is also used as a neurotransmitter in the saccular macula (Potter et al. 1986). Otolith forming cells, yet to be positively identified (Mugiya 1974; Dale 1976; Dunkelberger et al. 1980; Saito 1984), synthesize the precursor of the matrix and secrete it into the lumen. The precursor may then deposit on the otolith after further biochemical modification.

The present study showed the presence of a time-lag between the matrix biosynthesis in the saccular tissue and its deposition on the otoliths. However, this does not necessarily mean that these two processes are separated in phase. In this study, calcification and matrix formation were measured in terms of "instantaneous" growth rates (Ottaway 1978). Therefore the maximum deposition of organic matrix on otoliths at night must be accompanied by the active biosynthesis of the matrix in the cellular level and its consecutive secretion into the lumen, which may rather reduce the radioactivity in the saccular tissue. The high radioactivity in the tissue at dusk might result from the accumulation of the newly synthesized matrix owing to the reduction of its transport to the otoliths. These results suggest the presence of at least three different phases in otolith matrix formation: the active synthesis of matrix proteins on the cellular level with its reduced deposition on the otoliths, active synthesis with active deposition, and inactivity in both synthesis and deposition.

Mugiya (1984) reported that the profile of diurnal otolith calcification was antiphasal between the summer and winter solstices in rainbow trout. In the winter experiment, the peak and the nadir of calcium deposition on otoliths came at 1600 h and 0400 h, respectively; while in the present winter experiment the peak at 1600 h decreased to the nadir earlier, at 2200 h, followed by a slight increase at 0400 h. Although there is a difference in the time-related profiles, the results of both experiments mainly showed that otolith calcification slowed down after the onset of darkness and remained relatively inactive until the next sunrise.

Molluscan nacre shows a laminar structure resulting from alternate accumulation of organic

matrix and calcium carbonate crystals. In the development of these bipartite structures, matrix deposition on growing crystals is known to interrupt further crystal growth (Wilbur 1980). This results in the alternate formation of calcium-rich and matrix-rich layers. In such cases, the matrix may have opposite functions in controlling crystal growth: as an inhibitor for the crystal growth along the C-axis and as a nucleator for the formation of the next crystal layer (Crenshaw 1982). The matrix appears to play a key role in controlling the formation of these different layers. Although this sequence is likely to be the case for otolith increment formation (Wilbur 1980), the rate of calcium deposition on otoliths appears to be closely related to the level of serum calcium, which is regulated by the action of hypercalcemic and hypocalcemic hormones (Oguro and Pang 1982). Serum calcium has been suggested as a trigger for otolith calcification through the calcium-calmodulin system (Mugiya 1986). Although Pickford (1953) found that hypophysectomy resulted in no otolith growth in killifish, what exactly controls the rate of matrix deposition on otoliths remains unknown.

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ESTIMATES OF THE LANDED CATCH OF RIGHT (AND OTHER WHALEBONE) WHALES IN THE AMERICAN FISHERY, 1805-1909

PETER B. BEST[1]

ABSTRACT

Using a combination of the numbers of bowhead, right, humpback, and gray whales listed for particular voyages by C. H. Townsend, and the declared returns of whale oil and whalebone from the same voyages as listed by A. Starbuck and R. B. Hegarty, mean oil and whalebone yields per whale are calculated and temporal trends in these yields investigated for each species. These are then used to obtain an estimate of the total landed catch for each 5-year period from 1805 to 1909, using the species composition from Townsend's lists and adjusting it upwards from the ratio of oil or bone production for Townsend's sample to the total known importation of these products to the United States for the same period. An alternative estimate is based on the catch per voyage in Townsend's sample, stratified by voyage-type (sperm, whalebone, or mixed), and prorated up by the number of whaling voyages of the same type as listed by Starbuck and Hegarty. The two methods produced estimates of the landed catch by American-registered vessels between 1805 and 1909 of 29,748-30,313 bowhead, 70,325-74,693 right, 14,164-18,212 humpback, and 2,665-3,013 gray whales.

Between 1715 and 1928, whaling vessels from American ports are estimated to have made 13,927 voyages, mostly under sail, in their worldwide pursuit of oil and whalebone (Sherman 1965). In 1846, at the peak of the fishery, the American whaling fleet comprised over 735 vessels displacing 233,189 tons (Hohman 1928). Because of the essentially unregulated and competitive nature of the enterprise, no systematic recording or collection of catch statistics was ever initiated for this very extensive fishery.

In 1875, Alexander Starbuck began to compile a list of the returns of whaling vessels from American ports from 1715, a task continued to the end of the fishery in 1928 by Hegarty (1959). These publications list for each voyage the vessel's name, class, tonnage, captain, managing owner or agent, destination, dates of sailing and arrival, and the results of the voyage in barrels of sperm or whale oil and pounds of whalebone. Numbers of whales taken are not given, but this did not prevent Starbuck (1878) from making his own calculations. In a footnote to his table J, which listed quantities of oil and whalebone imported into the United States from 1804 to 1876, Starbuck stated that

> Scammon estimates that sperm whales will average 25 and right whales 60 barrels of oil, and of the former 10 and of the latter 20 per cent of those killed are lost. Upon that basis the above amounts of oil would represent the slaughter of 225,521 sperm, and 193,522 right whales.

The latter figure has frequently been quoted as representing the size of the historical take of right whales (sometimes incorrectly for the period 1804 to 1817, an error apparently originally perpetrated by Harmer [1928], who also inferred that the entire take was of southern right whales). It is clear however that the landings of oil not only included production from both northern and southern right whales, but also from bowhead, humpback, and gray whales, species for which Starbuck (1878) made no allowance in his original calculation.

In this paper, an attempt has been made to revise Starbuck's calculations to account for the species composition of the catch, to extend his analysis forward in time using importation figures provided by Hegarty (1959), and to use whalebone as well as oil production. An independent method of estimating the landed catch using the catch per voyage has also been developed.

The motivation for this paper arose from the International Whaling Commission meeting on the past and present status of right whales, held in Boston in 1983, where the need for an improved estimate of the size of the American catch of right whales became apparent (Brownell et al. 1986).

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MATERIAL AND METHODS

From logbook extractions, Townsend (1935) tabulated the numbers of sperm, bowhead, right, humpback, and gray whales taken per voyage by 744 whaleships (mostly American) between 1751 and 1925. These figures include not only the whales processed but also those killed and brought alongside but subsequently lost before processing; these statistics have thus been termed the "landed catch" in this paper. The numbers of right whales are listed by ocean (i.e., North and South Pacific, North and South Atlantic, and Indian Oceans). In all, 53,877 whales are listed from 1,665 voyages. Excluding non-U.S. vessels, 16,837 baleen whales were taken in a total of 1,651 voyages, of which 636 were only sperm whaling voyages. The species composition of the baleen whale catch as extracted by Townsend has formed the basis of all the analyses performed in this paper, and is henceforward referred to as the "Townsend sample".

Some of the original work sheets used by Townsend in his 1935 paper were discovered in 1978 in the library of the Osborne Laboratory of the New York Aquarium. These comprise voyage abstracts giving the date, ocean, geographical position, number, and species of each whale landed, together with remarks such as "found dead", "cow and calf", etc.; about half of the work sheets are in the original handwriting of the compiler(s), while the remainder consist of typewritten copies. The abstracts cover voyages by most vessels whose names started with letters A through J (bark *A. Houghton* to brig *Juno*). Because some errors apparently occurred between the original abstracts and the final printed version (Schevill and Moore 1983), the catch data for the 438 voyages on which baleen whales were landed and for which abstracts were available has been checked against the figures tabulated by Townsend (1935). Errors were found in 32 voyages (or about 7% of the total) and corrected. The abstracts examined represent a landed catch of 6,982 baleen whales, or roughly 41% of the total Townsend sample.

Mean oil and whalebone yields per whale have been obtained by comparing the numbers of whales caught on a voyage (as listed by Townsend) with the amount of whale oil or whalebone landed for the same voyage (as listed by Starbuck (1878) or Hegarty (1959)). To avoid complications created when more than one baleen whale species was taken, only voyages where a single baleen whale species was taken have been analyzed. Because of suspected differences in size (and so presumably in yields of products) between North Pacific right whales and those from other seas (Omura 1958), they have been considered as a separate "species" for the purposes of this section. In order to reduce the amount of variation in yield and to avoid situations where Townsend seems to have had access to only a partial log of the voyage, only voyages on which 10 or more animals of that species were taken have been used (or roughly 20% of Townsend's sample of voyages on which whalebone whales were taken). Oil or bone sent home or sold abroad has been included where it is known; as Starbuck (1878) has pointed out, that sold abroad was not always accounted for.

Figures for the total annual importation of oil and whalebone into the United States have been taken from Starbuck (1878) and Hegarty (1959).

For the catch per voyage analysis, the voyages in the Townsend sample have been stratified according to type, either sperm (when only that species was landed), whalebone (when no sperm whales were included in the catch), or mixed (when both sperm and whalebone whales were taken). The numbers of such cruises have then been adjusted upwards by the numbers of such voyages found in the Starbuck/Hegarty compilation, where vessels were identified as sperm whalers if they were reported as returning with or sending home only sperm oil, as whalebone whalers if they only reported whale oil and/or bone, and as mixed whalers if they returned with or sent home both whale oil/bone and sperm oil. Two additional classes were recognized in the Starbuck/Hegarty compilation: "clean" voyages and "incomplete" voyages. Clean voyages were those entered as such by Starbuck (1878), but as Hegarty (1959) did not continue this practice, any of the voyages he listed that were completed but for which no production was reported were scored as "clean". Both authors listed several voyages that were not completed owing to fire, shipwreck, the vessel being condemned, etc., and for which no production was reported. These voyages were scored as "incomplete", and half their number was allocated on a prorata basis as either sperm, whalebone, mixed, or clean whalers, based on the proportions of these categories in the sample of completed voyages. The other half of the incomplete voyages was discarded, the assumption being that such voyages were on average probably half as successful as those completed and that Townsend (1935) was unlikely to have had access

to the logbooks of many of them. Incomplete voyages comprised 9.6% of those listed by Starbuck (1878) and Hegarty (1959).

A "plus minus" figure following any estimate refers to one standard error.

Values given for the coefficient of variation (CV) have been obtained using variances calculated by the jackknife method (using one voyage as the sampling unit). No attempt has been made to calculate coefficients of variation for the final estimates because 1) certain independent components of the variance could not realistically be assessed (e.g., variation in the proportion of a particular species in the total catch to that in the Townsend sample from one 5-yr period to the next) and 2) any biases in the data are likely to be of greater magnitude than statistical errors resulting from sampling variation.

ESTIMATES BASED ON PRODUCTION

The number of baleen whales landed by American whalers as extracted by Townsend (1935) is listed by five yearly period in Table 1. If Townsend's data for a particular voyage covered more than one calendar year, the catch would be entered against the later date, as this was more likely to correspond to the importation figures used as a basis for reconstruction of the catch. A total landed catch of 4,963 bowhead, 8,293 right, 2,879 humpback, and 569 gray whales was recorded for the period 1805-1914.

Average Oil Yield Per Whale

Right Whales

There were 147 right whale cruises producing oil yields ranging from 22.5 to 219 barrels (Fig. 1). As expected, the 17 voyages that took North Pacific right whales had higher yields (83 to 219 barrels) than the 130 taking right whales elsewhere (22.5 to 150 barrels), and so have been considered separately.

There was no significant trend in oil yield per whale during the period in which North Pacific right whales were taken ($b = -1.15 \pm 0.91$, $t = 1.27$, $P > 0.20$), so the overall average oil yield per whale of 41,645/341 or 122 barrels (CV = 0.063) has been used. This compares with published averages of 125 barrels, males making 60 to 100 and females 100 to 250 barrels (Clark 1887a), and 130 barrels (Scammon 1874).

There appeared to be a distinct decline in the oil yield of right whales on other grounds after 1882 ($b = -1.09 \pm 0.30$, $t = 3.60$, $P < 0.02$). Oil yields after this date have therefore been calculated from the least squares estimating equation fitted to the data:

$$y = 64.78 - 1.090\ (x - 1882)$$

TABLE 1.—Five-year compilation of whalebone whale catches from Townsend (1935).

Period (arrival)	Bowhead	Northern right		Southern right			Humpback	Gray	Total
		Atl.	Pac.	Atl.	Pac.	Ind.			
1805–1809	—	—	—	43	—	—	—	—	43
1810–1814	—	—	—	—	—	—	—	—	—
1815–1819	5	—	—	3	22	—	2	—	32
1820–1824	—	—	—	81	—	—	—	—	81
1825–1829	—	—	—	269	—	—	1	—	270
1830–1834	—	—	—	940	71	72	5	—	1,088
1835–1839	—	—	—	761	356	477	96	—	1,690
1840–1844	—	—	324	53	516	505	66	—	1,464
1845–1849	91	—	1,088	55	349	129	89	—	1,801
1850–1854	1,101	—	165	88	34	48	84	6	1,526
1855–1859	1,238	1	235	53	72	83	242	65	1,989
1860–1864	650	9	117	109	104	48	193	205	1,435
1865–1869	717	2	107	108	25	43	124	215	1,341
1870–1874	471	—	15	45	18	46	774	70	1,439
1875–1879	104	6	13	54	1	13	380	8	579
1880–1884	119	4	1	77	26	—	619	—	846
1885–1889	76	5	38	53	72	3	171	—	418
1890–1894	86	—	3	38	13	—	22	—	162
1895–1899	183	1	12	7	—	6	10	—	219
1900–1904	74	—	6	11	—	2	1	—	94
1905–1909	33	—	1	10	6	71	—	—	121
1910–1914	15	—	—	26	—	25	—	—	66
Total	4,963	28	2,125	2,884	1,685	1,571	2,879	569	16,704

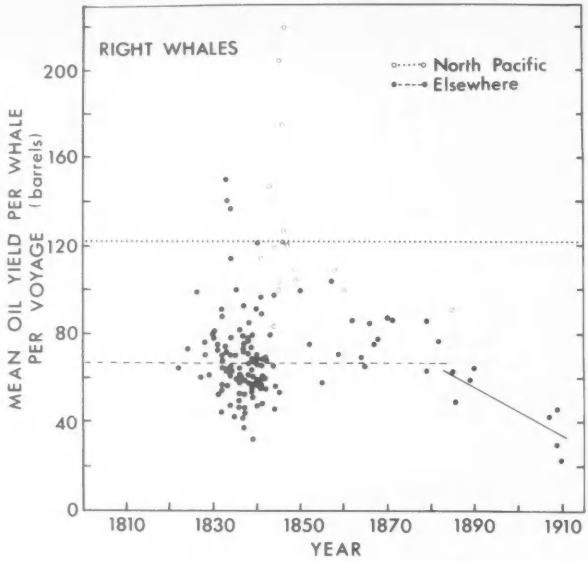

FIGURE 1.—Mean oil yield per whale for right whales landed on U.S. voyages from 1822 to 1910.

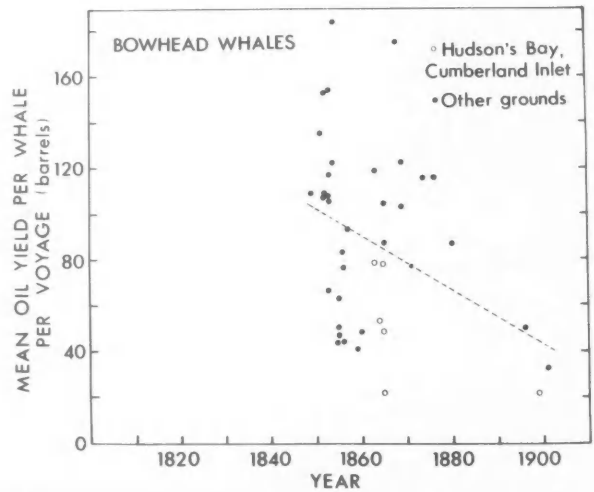

FIGURE 2.—Mean oil yield per whale for bowhead whales landed on U.S. voyages from 1849 to 1901.

where x = year of arrival (>1882) and
y = average oil yield (barrels).

This produces a decline from 63.7 barrels in 1883 to 34.2 barrels in 1910.

Prior to 1883 there was no significant trend with time ($b = 0.16 \pm 0.16$, $t = 1.01$, $P > 0.2$), so the average overall oil yield of 206,328/3,080 or 67 barrels (CV = 0.024) per whale has been used. Right whales in the South Atlantic were said to yield (when full grown) from 40 to 60 barrels of oil if male and 60 to 80 barrels if female, or about 60 barrels on average. Those in the South Pacific and Indian Oceans were said to be smaller, averaging 40 barrels if male and 60 barrels if female (Clark 1887a). Eleven right whales taken in the Indian Ocean averaged 59 barrels, with a maximum of 80 barrels (Wray and Martin 1983). In a sample of 29 right whales taken in the North Atlantic, Reeves and Mitchell (1986) found a range of oil yields from 6.5 to about 100 barrels with a mean of 58 to 59 barrels. These figures all agree fairly well with the calculated values used here: the decline in yield after 1883 may reflect market considerations and the relative value of oil and whalebone (see below).

Bowhead Whales

Oil yield data were available for 39 voyages on which 987 bowhead whales were taken; six voyages were to "Hudson's Bay" or "Cumberland Inlet" (Fig. 2). The latter voyages had generally lower oil yields (22 to 79 barrels) than the other grounds (32 to 184 barrels), possibly reflecting differences in distribution of size groups, or the effects of greater depletion. However, as no distinction was made in Townsend's (1935) tabulations between bowhead whales caught on different grounds, the data set has not been subdivided. Oil yields seemed to decline throughout the period of the fishery ($b = -1.19 \pm 0.48$, $t = 2.46$, $P < 0.02$), so for any particular year the mean oil yield has been calculated from the estimating equation:

$$y = 105.11 - 1.1892\,(x - 1848)$$

where x = year of arrival (>1848) and
y = average oil yield (barrels).

The slope of this regression is very sensitive to the three data points after 1890; their exclusion results in a much slower, nonsignificant rate of decline ($b = -0.58 \pm 0.73$, $t = 0.79$, $P > 0.20$). However, in view of the decreasing oil yields with time found by other workers and the economic incentives after 1880 that favored the collection of whalebone rather than whale oil (see below), the regression coefficient shown in Figure 2 has been retained.

This produces a decline from 103.9 barrels in 1849 to 31.4 barrels in 1910; yields before 1849 (for which no data exist) are taken as 103.9 barrels per whale.

According to Scammon (1874), bowhead whales could be classified into three types, yielding on average 200 barrels, 100 barrels, and 75 barrels of oil. Bowhead whales in the Davis Strait were said to average about 120 barrels (males 100, females 140), but had decreased in size "of late years". In the Okhotsk Sea, cows averaged about 130 barrels and the bulls about 90 barrels, but once again the whales had been much smaller "during recent years" (Clark 1887a). Oil yields for 333 whales from the Western Arctic stock listed by Bockstoce and Botkin (1983) averaged 112.4 barrels. These averages are all somewhat higher than the yield calculated here, but (with the exception of the last) they referred principally to the commencement of the fishery. Bockstoce and Botkin (1983) have also documented a decline in the size of bowhead whales taken over time, but the regression of barrels per whale per year has a somewhat smaller slope (−0.61 barrels per year) than in the present case: the mean yield declined from about 119 barrels in 1850 to about 70 barrels in 1900 (cf 43 in the present data). This difference may simply reflect a different measurement—Bockstoce and Botkin apparently only considered the yield of animals for which a barrel-estimate was made by the whaling vessel so that animals may have been excluded if no oil was rendered from them. The present analysis however considers all whales taken on a voyage (whether processed into oil and whalebone or not), so that it is not surprising that its figures are somewhat lower than for previous estimates. An oil yield as low as 49 barrels per whale was calculated for bowhead whales in Hudson Bay between 1860 and 1890 (Ross 1974).

Humpback Whales

Oil yield data were available for 29 cruises on which 1,137 humpback whales were taken (Fig. 3). There was no significant trend with time ($b = 0.31 \pm 0.19$, $t = 1.58$, $P > 0.10$), so the aver-

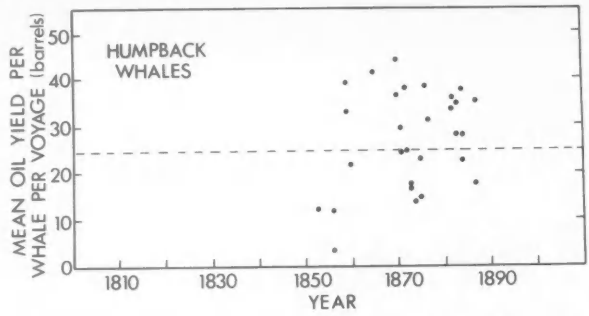

FIGURE 3.—Mean oil yield per whale for humpback whales landed on U.S. voyages from 1853 to 1887.

age overall oil yield of 27,797/1,137 or 24.4 barrels (CV = 0.110) per whale has been used throughout. According to Scammon (1874), humpback whales varied more in their production of oil than all other rorquals. Some individuals yielded only 8 or 10 barrels, whereas others gave up to 75 barrels; large females yielded on average 40 barrels. Mitchell and Reeves (1983) used an average of 25 barrels per whale, although individual whales yielded from 5 to 85 barrels each. The value calculated here is thus in reasonable agreement with previous estimates.

Gray Whales

There were no cruises in Townsend (1935) on which gray whales were the only baleen whale species taken, on which at least 10 animals were landed, and for which production figures were available in Starbuck (1878). Consequently the average production figure of 35 barrels per whale estimated by Henderson (1972) has been used throughout.

Average Yield of Whalebone Per Whale

Average yields of whalebone have been calculated essentially the same way as for oil. However, as Starbuck (1878) pointed out, in the earlier years (before about 1844/45), reports of the amount of bone taken were only occasional:

> Most of that commodity was imported prior to 1840 in New London and Sag Harbor ships, its value being so low that captains of vessels from many of the other ports did not care to be encumbered with it. For this reason a large amount of bone was brought home which it is impossible to properly accredit.

Figures for whalebone landings were listed for 94 to 95% of the voyages on which bowhead or North Pacific right whales were taken, but for only 30 and 24% of the voyages taking other right and humpback whales respectively. Two alternative (and probably extreme) assumptions can therefore be made: A) that only those vessels listed as landing whalebone actually did so, or B) that all vessels taking baleen whales retained the whalebone to the same extent as those for which whalebone production was reported. Average whalebone yields per whale (and trends therein) have been calculated here under both assumptions A and B (Figs. 4-7).

Right Whales

Of the 17 voyages on which 10 or more right whales were taken in the North Pacific, whalebone production was reported for 16 (Fig. 4). There was no significant trend in bone yield per whale in all 17 voyages ($b = -6.36 \pm 13.98$, $t = 0.46$, $P > 0.6$) or in the 16 for which bone production was declared ($b = -12.84 \pm 12.14$, $t = 1.06$, $P > 0.3$). Consequently overall mean yields of 384,134/341 or 1,126 lb (CV = 0.098) whalebone (assumption A) and 384,134/323 or 1,189 lb (CV = 0.082) whalebone (assumption B) have been used. According to Clark (1887a), whalebone yield in North Pacific right whales averaged about 1,000 lb per 100 barrels (equivalent to a yield of 1,250 lb for an average whale), while Scammon (1874) gave a range of 1,000 to 1,500 lb.

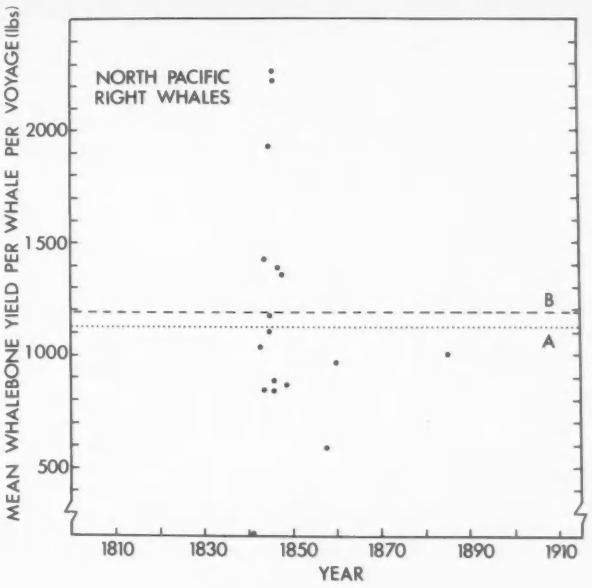

FIGURE 4.—Mean whalebone yield per whale for North Pacific right whales landed on U.S. voyages from 1841 to 1885 (A = assuming only those vessels listed as landing whalebone actually did so, B = assuming all vessels taking whalebone whales retained the whalebone to the same extent as those for which whalebone production was reported).

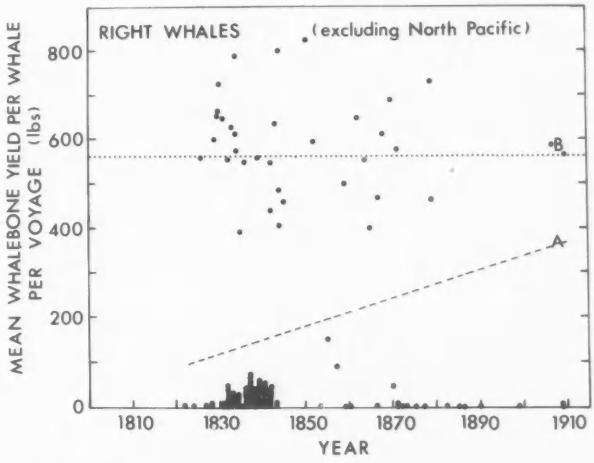

FIGURE 5.—Mean whalebone yield per whale for right whales landed on U.S. voyages (other than in the North Pacific) from 1822 to 1910 (A = assumption A, B = assumption B).

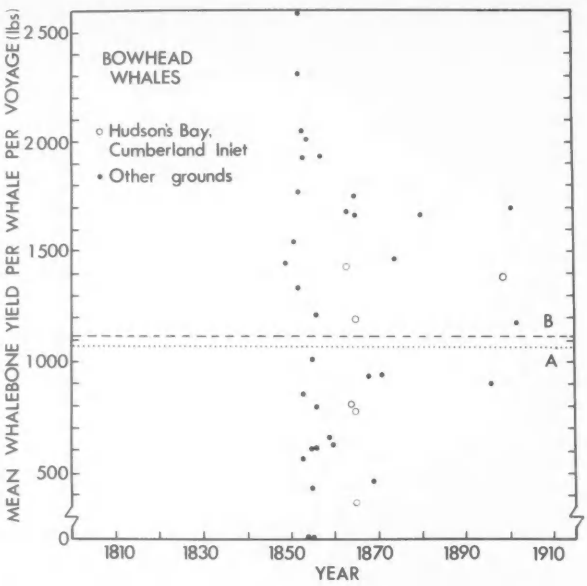

FIGURE 6.—Mean whalebone yield per whale for bowhead whales landed on U.S. voyages from 1849 to 1902 (A = assumption A, B = assumption B).

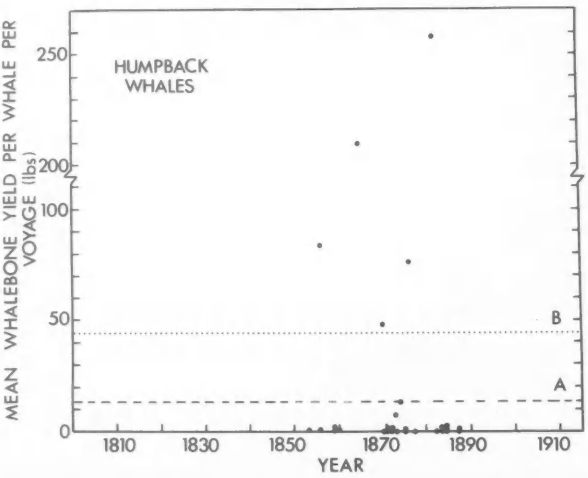

FIGURE 7.—Mean whalebone yield per whale for humpback whales landed on U.S. voyages from 1853 to 1887 (A = assumption A, B = assumption B).

Present calculations are therefore close to these estimates.

Of the 127 voyages taking right whales on grounds other than the North Pacific, bone yields were available for only 37 (Fig. 5). For all 127 cruises there was a significant trend in mean yield with time ($t = 2.40$, $P < 0.02$), so annual values under assumption A were calculated from the least squares estimating equation:

$$y = 92.51 + 3.11\ (x - 1821)$$

where x = year of arrival (>1821) and
y = average whalebone yield (lbs).

This equation produces a yield of 96 lb per whale in 1822 and a yield of 370 lb per whale in 1910: yields before 1822 (for which no data exist) are taken as 96 lb per whale.

For the 37 cruises where bone production was declared, there was no significant trend in average yields with time ($b = -0.67 \pm 1.26$, $t = 0.53$, $P > 0.6$), so the overall mean yield of 497,840/884 or 563 lb (CV = 0.043) of bone per whale has been used under assumption B. This agrees well with a calculated mean of 629 lb and adult range of 250 to 330 kg (550 to 726 lb) for right whales from South Africa (Best 1970) and the North Atlantic (Collett 1909), respectively. Clark (1887a) stated that right whales in the South Atlantic yielded on average about 300 lb of bone per 100 barrels of oil in the male and 400 to 600 lb per 100 barrels in the female (equivalent to an actual yield of about 180 lb per whale in the male and 240 to 360 lb in the female). Although he claimed that right whales in the Indian Ocean were smaller than those in the South Atlantic, average whalebone yields are given as 240 lb for males and 360 lb for females. It is not clear why Clark's figures are somewhat lower than the others quoted here.

Bowhead Whales

Of the 39 voyages taking bowhead whales that were analyzed, 37 included reference to landings of whalebone (Fig. 6). There was no significant trend in the mean yield of whalebone per whale, either under assumption A ($b = 0.03 \pm 7.19$, $t = 0.005$, $P > 0.9$) or B ($b = -2.87 \pm 6.66$, $t = 0.4305$, $P > 0.6$). Overall mean yields can therefore be calculated as 1,060,911/993 = 1,068 lb (CV = 0.098) per whale (assumption A) or 1,060,911/949 = 1,118 lb (CV = 0.095) per whale (assumption B). According to Clark (1887a), the yield of bone in bowhead whales from the Atlantic-Arctic grounds averaged about 1,300 lb to 100 barrels of oil (or about 1,560 lb per whale), whereas in the Okhotsk Sea the yield was about 1,500 lb to 100 barrels of oil (or about 1,650 lb per whale). In both areas, however, Clark commented that whales found there "during recent years" were much smaller than those taken at the beginning of the fishery; the values given above referred essentially to the start of the fishery. Ross (1974) calculated the average yield for a bowhead whale from the Hudson Bay stock as 1,065 lb, later revised to 916 lb (Ross 1979). For whales from the Davis Strait stock, the average yield was calculated as 1,392 lb (Ross 1979). Present estimates are therefore within the range of those given previously.

Humpback Whales

Of the 29 voyages taking humpback whales that were analyzed, only 7 had associated whalebone production (Fig. 7). There was no significant trend in the mean yield of whalebone per whale, either under assumption A ($b = -0.21 \pm 1.20$, $t = 0.17$, $P > 0.8$) or B ($b = 1.95 \pm 5.12$, $t = 0.38$, $P > 0.7$), so the relevant overall means have been used, i.e., 15,116/1,137 = 13 lb (CV = 0.416) under assumption A and 15,116/345 = 44 lb (CV = 0.652) under assumption B. Scammon (1874) stated that humpback baleen was of inferior quality, but could be collected at a rate of about 400 lb per 100 barrels of oil; this would be equivalent in current calculations to a yield of 98 lb whalebone per whale. Mitchell and Reeves (1983) confirmed that baleen from humpback whales was generally considered of poor quality, but pointed out that it was occasionally marketed.

Gray Whales

There were no voyages available on which 10 or more gray whales were taken and for which whalebone production was declared. According to Henderson (1972:84):

> Unlike the valuable baleen of the right and bowhead whales, whalebone from the gray never became an important part of the catch . . . little bone was recorded in the cargos of the gray whaling vessels. The few recorded cargos of gray whalebone to arrive in San Francisco and

San Diego did not appear until gray whaling was in decline and the price of right and bowhead whalebone had risen considerably after the mid 1860s.

Rather than adopting an arbitrary value for the average whalebone yield of gray whales, it has been taken as zero. This means that estimates of the size of the catch of other species using whalebone production may be correspondingly overestimated by an unknown but probably small amount. However, as whalebone production is used only to estimate the landed catch from 1880 onwards (see below), and there are no gray whales in the logbook sample after this date, the practical effect of this assumption is minimal.

Estimates of Total Landed Catch of Whalebone Whales

Figures for the importation of whale products into the United States have been based on table J of Starbuck (1878), supplemented by data in Hegarty (1959). As pointed out by Starbuck, it would appear from a comparison of imports and exports from 1804 to 1817 that much oil and bone must have been imported which was not credited to any port, and thus did not appear in table J. After 1817 exports as listed by Starbuck totalled 0.373 of imports for whale oil and 0.697 for whalebone. It was presumably these figures that led Starbuck (1878) to propose that exportation of whale oil and bone for 1804 to 1817 represented one-third and two-thirds respectively of the importation, and I have followed his proposal in adjusting the figures for 1804 to 1817 upwards on a prorata basis. The validity of this assumption is of course unknown.

Inspection of table K in Starbuck (1878) also shows that importation figures for whalebone from 1838 to 1842 were "estimated" or "assumed", apparently at a rate of 10 lb of whalebone per barrel of oil, and may not therefore be very reliable. The data, summed by five yearly periods, are shown in Table 2.

In order to estimate the total landed catch for any 5-yr period, the catch of each species given in Table 1 has been multiplied by its mean yield of oil or whalebone (corrected for the relevant year of catch, if necessary, using the median year in any 5-yr period) and the resulting production figures summed. Comparison of this total with that in Table 2 for the same period then provides a scaling factor by which the catches in Table 1 have to be multiplied to obtain the total landed catch for that period. These scaling factors are shown in Table 2.

In two of the three data sets (those for oil and whalebone factor A), there was a tendency for the scaling factors to be particularly high at the beginning of the time series, indicating that logbook coverage (and hence the reliability of extrapolations) was poor in the earlier years. The great differences between the two scaling factors for whalebone before about 1845 suggests either that a lot of whalebone was not being collected from the whales taken, or that it was not possible to allocate imports of it to a particular port or vessel (Starbuck 1878). The low ratio of whalebone to whale oil imported from 1805 to 1834 (Table 2) would indicate that the former was the more likely. Given the unreliability of import figures for whalebone from 1804 to 1817 and between 1838 and 1842, this suggests that oil production figures would be a more appropriate measure of the landed catch before about 1845.

All three factors converge closely from 1855 to 1879, presumably indicating that full utilization was being made of both whalebone and whale oil. During this period the ratio of whalebone to whale oil imported ranged from 7.7 to 11.0, with a mean of 9.1 lb to a barrel of oil (Table 2).

After 1880 the factors tend to diverge again, but this time the divergence is mainly between

TABLE 2.—Five-year compilation of imports of whalebone and whale oil into the United States (from Starbuck 1878 and Hegarty 1959).

Period	Total U.S. imports		Ratio:	Scaling factors[1]		
	Whale oil (barrels)	Whalebone (lb)	Bone/ oil	Oil	Bone A	Bone B
1805–09	285,969	360,981	1.3	99.3	87.7	14.9
1810–14	96,759	151,921	1.6	—	—	—
1815–19	130,666	179,793	1.4	58.2	23.2	9.1
1820–24	246,793	429,447	1.7	45.5	55.4	9.4
1825–29	245,777	1,039,134	4.2	13.6	34.7	6.9
1830–34	680,729	1,846,907	2.7	9.4	13.4	3.0
1835–39	917,064	7,947,069	8.7	8.4	34.8	8.8
1840–44	1,032,080	10,159,715	9.8	9.1	19.0	10.2
1845–49	1,324,305	14,073,773	10.6	7.4	9.9	8.3
1850–54	1,193,253	17,143,100	14.4	8.3	12.3	11.2
1855–59	985,480	10,854,100	11.0	5.9	6.6	6.0
1860–64	509,037	4,388,800	8.6	5.0	4.9	4.3
1865–69	390,415	4,045,575	10.4	4.1	4.4	3.9
1870–74	256,714	2,054,769	8.0	3.9	3.8	3.3
1875–79	152,907	1,176,690	7.7	6.5	7.8	6.2
1880–84	138,654	1,785,354	12.9	4.6	10.7	8.1
1885–89	134,438	1,989,176	14.8	5.9	10.7	9.4
1890–94	62,614	1,667,478	26.6	7.6	15.0	12.9
1895–99	21,531	1,067,130	49.6	2.0	5.0	4.7
1900–04	17,175	614,830	35.8	4.0	6.8	6.3
1905–09	15,710	460,100	29.3	3.5	6.8	5.3

[1]Rounded to one decimal place.

the oil factor and both whalebone factors. This is accompanied by a marked increase in the ratio of whalebone to whale oil imported, to a peak of 49.6 lb to a barrel of oil from 1895 to 1899 (Table 2). It is assumed that over this period whalebone was collected in preference to whale oil, as described by Ross (1974) for bowhead whales:

> . . . with a dramatic rise in the price of whalebone the oil diminished to less than 20% of the value of a whale after 1890 . . . . As a result whaling masters intensified the search for bone; . . . the crews simply stripped away the baleen, which was readily transportable, and left the rest of the carcass, including the bulky blubber, to rot. Oil returns, therefore, do not accurately reflect the number of whales killed in the late decades of whaling.

It is apparent that after 1880, whalebone production would be a more accurate measure of the total landed catch.

The economic basis for these shifts in interest is clearly shown by the average prices of whale oil and whalebone imported into the United States each year from 1804 to 1909 (Starbuck 1878; Hegarty 1959). These have been used to calculate the relative contribution of whalebone to the total value of a right whale, assuming a ratio at maximum utilization of 10 lb of bone to a barrel (= 31.5 gal) of oil per whale (Table 3). Whalebone made a relatively minor contribution to the value of a whale (<20%) up to 1839, ranged from 20 to 34% between 1840 and 1874, but increased rapidly in value thereafter to a peak of 80.8% in 1905-09.

TABLE 3.—Prices paid for whale products imported into the United States and the relative value of whalebone from a right whale.

Period	Average price (US$)		% Contribution whalebone in total value of adult right whale
	Whale oil (per gal)	Whalebone (per lb)	
1805–1809	0.48	0.08	5.0
1810–1814	0.64	0.09	4.2
1815–1819	0.59	0.11	5.6
1820–1824	0.32	0.12	10.6
1825–1829	0.29	0.20	18.0
1830–1834	0.29	0.17	15.7
1835–1839	0.37	0.21	15.3
1840–1844	0.33	0.28	21.2
1845–1849	0.35	0.29	20.8
1850–1854	0.44	0.38	21.5
1855–1859	0.65	0.76	27.1
1860–1864	0.75	1.14	32.5
1865–1869	1.05	1.30	28.2
1870–1874	0.64	1.02	33.6
1875–1879	0.50	2.09	57.0
1880–1884	0.53	2.35	58.5
1885–1889	0.37	2.96	71.7
1890–1894	0.41	4.20	76.5
1895–1899	0.34	3.10	74.3
1900–1904	0.37	3.88	76.9
1905–1909	0.33	4.38	80.8
1910–1914	0.37	0.63	35.1

To conclude, oil production is considered the more accurate measure of the landed catch from 1804 to 1879, but whalebone production thereafter. With the high value of whalebone after 1879 (comprising more than half the total value of the whale), it is likely that it would be utilized whenever possible. Hence scaling factor B would be the more appropriate to use.

Using these factors, the total landed catch from the data tabulated by Townsend (1935) for American vessels only between 1804 and 1909 is estimated as 125,883 whales, comprising 30,313 bowhead, 74,693 right, 18,212 humpback, and 2,665 gray whales (Table 4). Of the right whales caught, 182 (0.2%) were taken in the North Atlantic, 15,374 (20.6%) in the North Pacific, 32,191 (43.1%) in the South Atlantic, 14,699 (19.7%) in the South Pacific, and 12,247 (16.4%) in the Indian Ocean.

ESTIMATES BASED ON CATCH PER VOYAGE

The use of production figures to estimate catches masks certain fundamental problems. According to R. C. Kugler (in litt. 6 March 1985), neither Starbuck nor Hegarty apparently made much effort to report a vessel's total take of oil. They relied primarily on newspapers, especially the Whalemen's Shipping List after it began publication in 1843. These reports, however, seldom gave more than the amount of oil on board at the time of the vessel's arrival. Only sporadically and inconsistently was shipped oil added in. This factor would mean that the mean oil yields per whale calculated here would be underestimated, and the total number of whales landed correspondingly overestimated. Nevertheless, the mean oil yields derived in this paper agreed reasonably well with contemporary opinion on how much a particular species should yield.

A further problem with the use of whale oil production is that the term "whale oil" was used to designate not only that from right and other species of whalebone whale, but also elephant seal and walrus oil. At certain periods the amounts landed of the latter were not negligible (Bockstoce and Botkin 1982; Busch 1985; Kugler in litt. 6 March 1985). However, it is not clear how much and in which direction this factor would affect the present analysis, depending on whether

TABLE 4.—Numbers of baleen whales landed by U.S. whalers, 1805–1909, based on oil production up to 1879 and whalebone production thereafter.

Period (arrival)	Bowhead	Northern right		Southern right			Humpback	Gray	Total
		Atl.	Pac.	Atl.	Pac.	Ind.			
1805–09	—	—	—	4,268	—	—	—	—	4,268
1810–14	—	—	—	—	—	—	—	—	—
1815–19	291	—	—	175	1,281	—	116	—	1,863
1820–24	—	—	—	3,683	—	—	—	—	3,683
1825–29	—	—	—	3,663	—	—	14	—	3,677
1830–34	—	—	—	8,804	665	674	47	—	10,190
1835–39	—	—	—	6,394	2,991	4,008	807	—	14,200
1840–44	—	—	2,957	484	4,709	4,608	602	—	13,360
1845–49	669	—	8,001	404	2,567	949	654	—	13,244
1850–54	9,103	—	1,364	728	281	397	694	50	12,617
1855–59	7,273	6	1,381	311	423	488	1,422	382	11,686
1860–64	3,250	45	585	545	520	240	965	1,025	7,175
1865–69	2,956	8	441	445	103	177	511	886	5,527
1870–74	1,815	—	58	173	69	177	2,983	270	5,545
1875–79	677	39	85	352	7	85	2,475	52	3,772
1880–84	958	32	8	620	209	—	4,985	—	6,812
1885–89	711	47	356	496	674	28	1,600	—	3,912
1890–94	1,108	—	39	490	168	—	284	—	2,089
1895–99	860	5	56	33	—	28	47	—	1,029
1900–04	468	—	38	70	—	13	6	—	595
1905–09	174	—	5	53	32	375	—	—	639
Total	30,313	182	15,374	32,191	14,699	12,247	18,212	2,665	125,883

the whale oil production of the voyages listed by Townsend was diluted to a greater or lesser extent with seal and other oil than the total production.

The catch-per-voyage analysis attempts to avoid the problems created by the incomplete reporting of the products of a voyage, and (at least partially) those arising from the dilution of whale oil with seal, walrus, and other oils.

In order to make some further correction for voyages that were entirely devoted to sealing, all voyages recorded as returning only elephant oil, or as "skinning voyages", or voyages labelled as sealing by Starbuck (1878) and Hegarty (1959) have been excluded. In addition, all voyages from the Connecticut ports of New London, Stonington, or Mystic that were recorded as being bound for S. Shetlands, Desolation, Falklands, Hurds Island, or Crozettes and that returned with whale oil but no whalebone have been omitted on the grounds that these were probably sealing voyages. This has resulted in a total omission of 141 voyages between 1804 and 1921.

Obviously this figure does not include all voyages on which seal oil was taken, as many seals were taken on combination sealing/whaling voyages. Between 1840 and 1890, an average 25% of "whaling" vessels leaving New London are said to have visited Desolation or Heard Island for elephant seals (Busch 1985), but of 110 voyages departing to these islands from New London during this period, 45 were reported as bringing back sperm oil and/or whalebone as well as "whale" oil (Starbuck 1878; Hegarty 1959).

Starbuck (1878) and Hegarty (1959) also listed a number of mixed voyages from other ports in which small amounts of whale oil were landed but no whalebone. While some of these might represent voyages on which whales with inferior whalebone (such as humpback or gray whales) were taken, other such small consignments of whale oil might have originated from seals or from "blackfish" (pilot whales *Globicephala* spp.). Pilot whales were sometimes taken by whalemen to supplement their cargoes, the oil being rated as common whale oil. Clark (1887b) listed 36 voyages on which from 2 to 200 barrels of blackfish oil was brought home, 33 (91.7%) of them bringing back 100 barrels or less. To investigate this further, mixed voyages on which 100 barrels or less of whale oil but no whalebone were landed (from Starbuck and Hegarty) were compared with the catch composition of the same voyages as given by Townsend (1935). Of 153 such voyages, baleen whales were reported as being taken on 55 (35.9%) voyages, with the proportion approaching 100% as the amount of whale oil approached 100 barrels (Table 5). Consequently for each 5-yr time period the number of mixed voyages reporting 100 barrels or less of whale oil but no whalebone was adjusted by the proportion of such voyages in Townsend's sample that were reported as taking

TABLE 5.—Proportion of mixed voyages by U.S. whalers landing small consignments of whale oil (but no whalebone) on which whalebone whales were taken.

Amount of whale oil reported (barrels)	Number of mixed voyages examined	Proportion of mixed voyages on which whalebone whales taken
1–10	53	0.113
11–20	19	0.263
21–30	18	0.444
31–40	14	0.500
41–50	11	0.364
51–60	10	0.300
61–70	12	0.750
71–80	8	0.750
81–90	2	1.000
91–100	6	0.833

baleen whales during the same period. This resulted in an effective conversion of 812 mixed voyages between 1805 and 1910 to sperm whaling voyages.

Because Starbuck (1878) and Hegarty (1959) listed voyages by the year of departure, the data in the catch-per-voyage analysis has been compiled against year of departure rather than (as was done for the production-based analysis) by year of arrival. The numbers of sperm, mixed, and whalebone voyages in Townsend's sample for each 5-yr period are given in Table 6, together with the scaling factors A1 and A2 for mixed and whalebone whalers respectively. The latter represent the ratio of the number of voyages of each type in the Townsend sample to the number of similar voyages in Starbuck/Hegarty for that period, after correction (as described above) for voyages believed to be sealing rather than whaling. These scaling factors are then applied to the total numbers of whales landed in the Townsend sample for that period and voyage-type, and the results for each voyage-type added to give the total number of each species for that period.

This analysis provides an estimate of the landed catch of whalebone whales from American vessels between 1805 and 1914 as 117,308, comprised of 29,788 bowhead, 70,343 right, 14,164 humpback, and 3,013 gray whales (Table 7). Of the right whales, 186 (0.3%) were taken in the North Atlantic, 14,480 (20.6%) in the North Pacific, 28,532 (40.6%) in the South Atlantic, 14,652 (20.8%) in the South Pacific, and 12,493 (17.8%) in the Indian Ocean.

Table 6.—Breakdown of Townsend's (1935) sample into voyage-type, with scaling factors (A1, A2) derived from numbers of such voyages in Starbuck (1878) and Hegarty (1959).

Period (departure)	Type of voyage: Sperm *n*	Mixed *n*	Mixed A1	Whalebone *n*	Whalebone A2	Total
1805–09	2	1	8.00	1	51.00	4
1810–14	1	0	—	0	—	1
1815–19	3	1	89.00	2	49.50	6
1820–24	6	3	23.67	1	117.00	10
1825–29	10	12	8.92	8	13.38	30
1830–34	29	47	6.00	11	18.09	87
1835–39	54	75	8.28	9	12.33	138
1840–44	56	88	8.64	4	28.75	148
1845–49	53	93	6.25	8	9.88	154
1850–54	51	102	5.74	9	16.56	162
1855–59	52	101	5.29	11	11.82	164
1860–64	49	54	4.76	16	3.06	119
1865–69	55	83	4.02	13	5.46	151
1870–74	30	31	4.77	4	6.75	65
1875–79	44	48	3.67	7	6.14	99
1880–84	29	28	4.32	11	11.91	68
1885–89	17	22	2.91	14	13.79	53
1890–94	18	16	2.56	8	18.50	42
1895–99	7	11	3.27	10	5.90	28
1900–04	22	9	2.67	10	4.70	41
1905–09	19	10	1.60	5	5.80	34
1910–14	11	2	2.50	3	2.67	16
Total	618	837		165		1,620

DISCUSSION

The two methods used give somewhat similar results, estimates of the landed catch differing by <10% in all cases except for South Atlantic right whales and humpback whales (where the production-based estimates exceeded the catch per voyage estimates by 13 and 29% respectively) and gray whales (where the catch per voyage estimate exceeded the production estimate by 13%).

Nevertheless, both sets of estimates are essentially derived from the same basic data (Townsend's sample), and a more fundamental problem with both analyses is how representative this sample was of the contemporary Yankee fishery. The 1,651 voyages examined by Townsend are equivalent to only 12% of the estimated total number of voyages made by American pelagic whalers (Sherman 1965), but the scaling factors in Tables 2 and 6 indicate that the coverage of voyages in some periods (particularly prior to 1830) was much less than this. Unless the logbook sample is truly random with respect to the species and numbers of whales taken, any simple reconstruction of the total catch therefrom is likely to be inaccurate.

The catch per voyage analysis included some stratification of the Townsend sample, so that extrapolations to the total fleet might be more representative. To this extent, therefore, the catch per voyage method might seem the more reliable,

TABLE 7.—Numbers of whalebone whales landed by U.S. whalers, 1805–1914, as calculated from the catch per voyage.

Period (departure)	Bowhead	Northern right		Southern right			Humpback	Gray	Total
		Atl.	Pac.	Atl.	Pac.	Ind.			
1805–09	—	—	—	1,849	—	—	—	—	1,849
1810–14	—	—	—	—	—	—	—	—	—
1815–19	248	—	—	149	1,958	—	178	—	2,533
1820–24	—	—	—	4,468	—	—	—	—	4,468
1825–29	—	—	—	3,617	535	—	63	—	4,215
1830–34	—	—	—	8,902	390	600	384	—	10,276
1835–39	—	—	149	5,662	5,190	5,561	285	—	16,847
1840–44	—	—	5,728	598	3,542	3,939	657	—	14,464
1845–49	2,148	—	5,578	515	1,485	421	669	—	10,816
1850–54	10,260	6	951	511	161	775	565	281	13,510
1855–59	5,454	48	1,221	429	579	501	2,317	1,279	11,828
1860–64	2,583	—	152	516	280	96	447	665	4,739
1865–69	3,215	11	434	354	105	342	2,153	755	7,369
1870–74	744	—	52	81	14	29	2,561	33	3,514
1875–79	417	40	16	400	95	40	1,801	—	2,809
1880–84	604	9	48	216	186	—	1,881	—	2,944
1885–89	729	69	90	113	122	9	134	—	1,266
1890–94	2,098	—	26	44	—	—	59	—	2,227
1895–99	715	3	16	23	—	26	10	—	793
1900–04	353	—	19	27	—	—	—	—	399
1905–09	180	—	—	40	10	154	—	—	384
1910–14	40	—	—	18	—	—	—	—	58
Total	29,788	186	14,480	28,532	14,652	12,493	14,164	3,013	117,308

but other problems (allowance for sealing voyages, correct allocation of incomplete voyages) may not have been adequately solved. Furthermore, even the stratification by voyage-type may have been insufficient to correctly portray the species composition of the total fleet; an alternative procedure might be to stratify by home port, but this would probably involve too fine a stratification for the size of the sample available.

A further problem identified with the Townsend sample is that there may be occasional misidentification or omission of catches (see Bockstoce and Botkin 1983). There is no indication of the extent of this problem (which would require checking Townsend's tabulations against the original journals), but it means that the accuracy of the extrapolations made in this paper may be adversely affected to an unknown degree.

Some independent estimates of the landed catch of various stocks have been made. Henderson (1972) estimated that 4,958-5,058 Californian gray whales were taken by pelagic whalers between 1846 and 1874, whereas calculations from the Townsend sample are that 2,665 to 3,013 gray whales were taken over the period 1850 to 1879. Henderson's estimate, however, includes the catches of non-U.S. vessels. From data in Henderson's table II it can be calculated that 64.9% of the 21,135 barrels of oil from Scammon's Lagoon between 1858 and 1873 were taken by U.S.-registered vessels. If this proportion is applied to the total catch, it means that U.S. pelagic whalers may have accounted for a landed catch of 3,218 to 3,283 gray whales. On this basis, calculations from the Townsend sample may be about 6 to 19% too low.

Bockstoce and Botkin (1983) calculated that 16,600 bowhead whales were taken from the Western Arctic population by the pelagic whaling industry between 1849 and 1914; this apparently included catches by non-U.S. vessels. Henderson has also estimated that the total catch of bowhead whales from the Okhotsk Sea stock between 1847 and 1867 was about 15,200 animals, with another 92 known to have been taken between 1867 and 1896 (Kugler 1984). About 90% of the voyages to the Okhotsk Sea between 1847 and 1867 were made by American whaleships, which if considered applicable to the catch would mean that they took about 13,760 bowhead whales from 1847 to 1896. Ross (1979) has estimated the catch of bowhead whales by American whalers in the Davis Strait from 1847 to 1891 as 413, and that in Hudson Bay from 1860 to 1912 as 532 animals; his figure for the Beaufort Sea of 794 bowhead whales between 1889 and 1908 is assumed to be included in Bockstoce and Botkin's calculations for the entire Western Arctic. Combining the data from Ross (1979), Bockstoce and Botkin (1983), and Kugler (1984) indicates a total bowhead

catch of 31,305 animals (some of which may have been taken by non-U.S. vessels). This is 3 to 5% higher than the total estimate of 29,788 to 30,313 bowhead whales from the Townsend sample.

Reeves and Mitchell (1986) have attempted to reconstruct the American pelagic catch of right whales in the North Atlantic during the nineteenth century. They document at least 116 right whales that were killed and processed by pelagic whales between 1855 and 1897. The present analysis indicates a total landed catch by U.S. whalers of 182 to 186 right whales over the same period.

These comparisons suggest that, apart from gray whales, the estimates of landed catch obtained in this paper are not unduly biased. They are, however, clearly only first approximations. A much more detailed approach, including examination of primary source material, is required before a more reliable assessment of the American catch of right whales can be made. In particular, there needs to be more adequate sampling of logbooks prior to 1830.

It should also be stressed that the figures produced here are estimates of the landed catch; further work is needed to determine the numbers of animals that were struck and lost, and the proportion of these that might have died, before an estimate of the total kill made by the American fishery can be made. Such research, requiring consultation of primary sources, is outside the scope of this paper. Nevertheless, a significant proportion of the landed catch of some species apparently consisted of whales found dead. In the Townsend abstracts examined here, there were records of 246 baleen whales processed that were found dead: 127 bowheads (6.3% of the landed catch), 103 right whales (2.9% of the landed catch), 5 humpback whales (0.4% of the landed catch), and 11 gray whales (or 4.4% of the landed catch). These figures might be underestimates if (as seems likely) not all the whales found dead were recorded as such in the logbooks or logbook abstracts. Most of these whales probably died as a result of whaling-related injuries. If so, this fact should be borne in mind when corrections are applied to the landed catch to account for whales struck and lost that subsequently died.

With no correction for animals dying after being struck and lost, the estimated number of right whales taken between 1805 and 1874 as calculated in this paper, 68,484 to 70,250 (of which 79% were southern right whales), is about one third of Starbuck's original estimate for the same period. This compares with an estimated total catch by French pelagic whalers between 1817 and 1868 of 11,000 right and bowhead whales (Du Pasquier 1986). Comparable figures for the British take are not yet available.

ACKNOWLEDGMENTS

I am indebted to M. A. Meÿer for the labor of extracting relevant information from Starbuck and Townsend's tables. Access to some of Townsend's original tabulations was very kindly provided by H. E. Winn (University of Rhode Island) and W. E. Schevill (Woods Hole Oceanographic Institution), and J. H. Prescott (New England Aquarium) and W. F. Perrin (National Marine Fisheries Service) assisted in arrangements for transport of the data at very short notice. Valuable comments on an earlier draft of this paper were received from an anonymous reviewer and J. M. Breiwick. Statistical advice was provided by D. S. Butterworth. Financial support for conducting this project came from the South African Department of Transport via the South African Scientific Committee for Antarctic Research.

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ESTIMATING DENSITY OF DOLPHIN SCHOOLS IN THE EASTERN TROPICAL PACIFIC OCEAN BY LINE TRANSECT METHODS

RENNIE S. HOLT[1]

ABSTRACT

Data were collected from aerial and research ship surveys to estimate density of dolphin schools in the eastern tropical Pacific using line transect (LT) theory. The surveys were conducted from 1977 through 1983. Several assumptions of LT theory were investigated for both aerial and ship data. Factors were developed to alleviate effects of suspected violations of the assumptions. I estimated densities from data stratified into an inshore area surveyed by planes and an offshore area surveyed by ships. The density estimate for the inshore area was 4.18 schools/1,000 km^2 and 2.04 for the offshore area. For the entire area, the density estimate was 2.71 schools/1,000 km^2. Adjustments for possible biases owing to adverse sea state and sun glare conditions increased the inshore estimate by 8% and the total area estimate by 4%.

The National Marine Fisheries Service (NMFS) is responsible for assessing the status of those dolphin stocks taken incidentally by tuna purse seiners in the eastern tropical Pacific (ETP) Ocean. Techniques used to assess these stocks (Smith 1979[2]) require estimates of school density, so density estimates were made in 1975 (Smith 1975[3]) and in 1979 (Holt and Powers 1982). Since 1979, NMFS has collected additional information to test the assumptions of its statistical methods and to further survey the areas inhabited by the dolphins. In this paper, I present analyses of data collected from 1977 through 1983 to determine density estimates of dolphin schools in the ETP. In addition, I investigate several factors which may bias the estimates.

To obtain estimates of density of dolphins (individuals) it is further necessary to consider school size, the proportions of various species in mixed schools, and areas inhabited by the various stocks. Estimation of these factors is complex; they are to be dealt with elsewhere and are not addressed in this paper.

MATERIAL AND METHODS

Surveys

Data used to calculate the density of dolphin schools were collected during several years. Aerial surveys were conducted in 1977 and 1979 (Fig. 1), and nine research ship cruises were made during 1977, 1979, 1980, 1982, and 1983 (Fig. 1). Most surveys were conducted between January and early April; one of the 1977 ship cruises was made in October and the two 1980 cruises were made from May through August.

A two-engine PBY amphibious patrol bomber was used in the 1977 aerial survey (SWFC 1978[4]), and a four-engine PBY bomber was used in the 1979 aerial survey (Jackson 1980[5]). Operating and viewing conditions aboard the two aircrafts were similar. Both planes cruised at 148-240 km/hour (80-130 kn) and had bubble-shaped waist windows. The PBY used in 1977 had a flat bow window which was shaped like an isosceles trapezoid. The 1979 PBY had a round bubble-shaped bow window. The round bubble window allowed

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2]Smith, T. 1979. Report of the status of porpoise stocks workshop (August 27-31, 1979). Southwest Fish. Cent. Adm. Rep. No. LJ-79-41, La Jolla, CA, 120 p.

[3]Smith, T. 1975. Estimates of sizes of two populations of porpoise (*Stenella*) in the eastern tropical Pacific Ocean. Southwest Fish. Cent. Adm. Rep. No. LJ-75-65, La Jolla, CA, 88 p.

[4]SWFC (Southwest Fisheries Center). 1978. Aerial survey trip report, January-June 1977. Southwest Fish. Cent. Adm. Rep. No. LJ-78-01, 73 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[5]Jackson, T. 1980. Report: Porpoise population aerial survey of the eastern tropical Pacific Ocean, January 22-April 25, 1979. Southwest Fish. Cent. Adm. Rep. No. LJ-80-01, 74 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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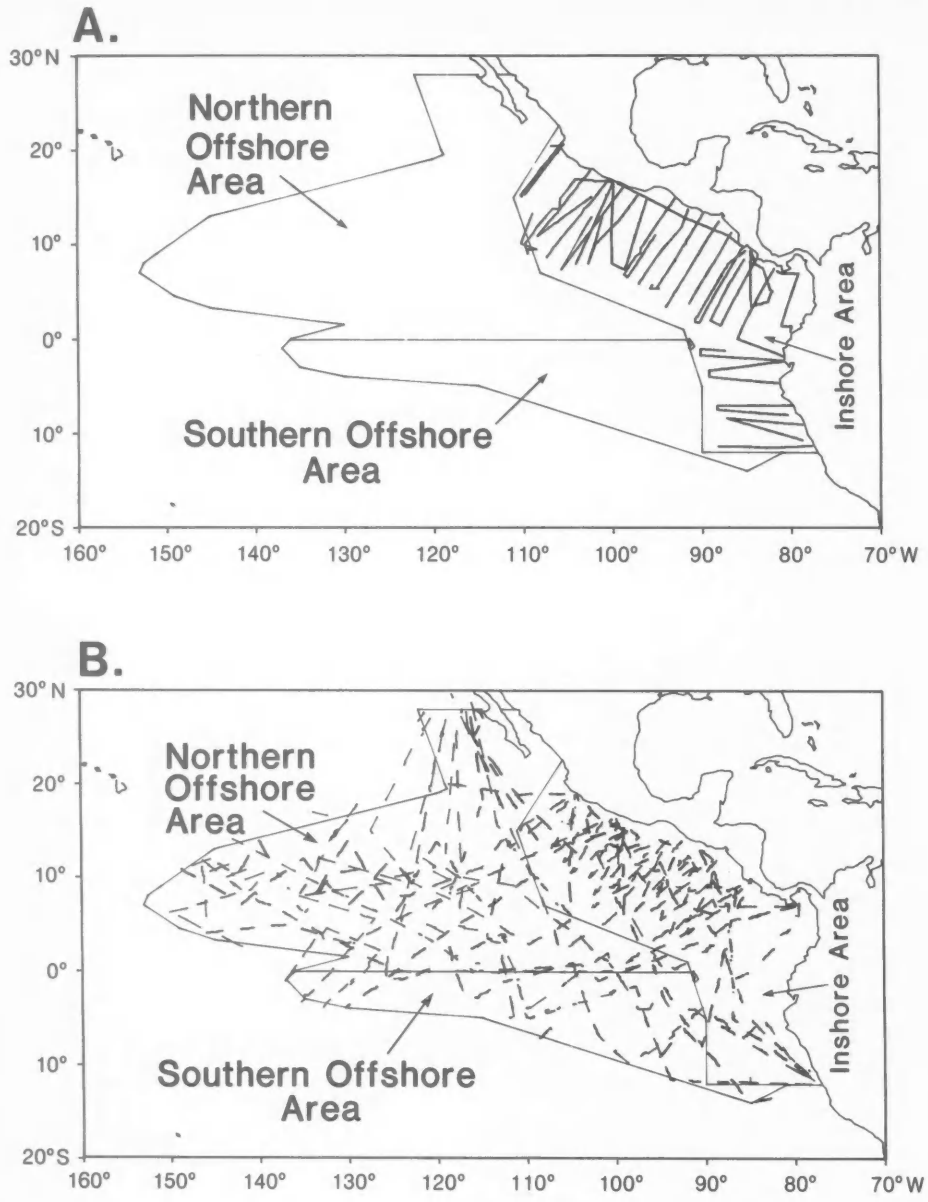

FIGURE 1.—Tracklines for 1977 and 1979 aerial (A) and combined 1977, 1979, 1980, 1982, and 1983 ship (B) surveys.

better lateral viewing, but both provided unobstructed forward and downward views.

Two research vessels were used to collect the shipboard data. The NOAA ship *David Starr Jordan* was used during all years and the NOAA ship *Townsend Cromwell* joined it in 1977, 1979, and 1980. Both vessels were similar in length and cruising ability. Binoculars used to locate animals were mounted approximately 10.7 m above the sea on the *Jordan* but were only 6.1 m above the sea on the *Cromwell*. In addition, observers aboard the *Jordan* used 20× binoculars during the 1977 surveys and 25× glasses on the rest of the surveys; observers aboard the *Cromwell* used only 20× glasses during their surveys. Consequently, viewing conditions were generally much better on the *Jordan*.

Study Area

Survey efforts traversed the combined range of ETP dolphin stocks defined by Au et al. (1979)[6]. The range was partitioned into "inshore" and "offshore" areas (Fig. 1). Airplanes were used to survey the inshore area, and ship surveys were conducted in both areas during each year, except during 1977 when ships surveyed only the offshore area.

Data Collection

Aerial Data

Data collecting procedures used during the aerial surveys are described by SWFC (fn. 4), Jackson (fn. 5), Holt and Powers (1982), and Cologne and Holt (1984)[7]. As the airplanes traversed predetermined tracklines (Fig. 1), the observers recorded schools on and to either side of the lines. Observers searched through the bow window and from windows located on either side of the plane. The bow observer was responsible for detecting schools on the trackline (a path underneath the plane 0.19 km wide). The searching mode was halted if environmental or oceanographic conditions restricted the observer's view of the trackline or when the plane was diverted from the trackline for closer examination of a school. Additional schools detected during these diversions were not included in the density analysis.

Sea conditions were measured on the Beaufort scale (Bowditch 1966), which ranged from very flat, glassy seas (Beaufort 0 conditions) to rough seas with numerous large, white-capped waves (Beaufort 5 conditions). Sun location was described by horizontal and vertical position relative to the bow observer (Holt 1983a). These were recorded for each segment of effort.

Biological and environmental data were recorded at each sighting (Holt and Powers 1982). Data included species identification, school size estimates, sea state, sun position, and perpendicular distance to the school from the trackline. School size estimates consisted of an observer's "best" estimate plus an estimate of the minimum and maximum range.

Ship Data

Shipboard collection procedures are described in the various cruise reports (unpublished documents available from the SWFC) and by Holt (1983b). Procedures and data recorded on shipboard surveys were similar to those for aerial surveys. Two observers used binoculars located on each side of the ship to search from directly ahead to abeam of their respective sides of the ship. Starting in 1979, sea state was recorded at the beginning of each effort segment (leg). Sun position was recorded during the 1982 and 1983 ship surveys.

The bearing (θ) and radial distance (r) to a school from the ship were recorded, and perpendicular distance (y) was then calculated as $y = r \sin \theta$. In surveys conducted before 1980, observers rounded estimates of sighting angles to multiples of 5° or 10°, and radial distances to multiples of 185 m (0.1 nmi) within the first 1.85 km (1 nmi), and to 0.93 km (0.5 nmi) multiples at larger distances (Fig. 2). During training, observers on the 1980 surveys were told of previous rounding inaccuracies and instructed to make estimates as precise as possible. However, they were still unable to make precise visual estimates of angles and distances for schools recorded at great distances from the ship (Fig. 2). During the 1982 and 1983 surveys, estimates of bearing were recorded using a 360° graduated washer attached to the base of the binoculars, and the radial distances were measured using a graduated reticle enclosed in the right eyepiece of the binoculars (Holt 1983b).

[6]Au, D., W. Perryman, and W. Perrin. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Southwest Fisheries Center Status of Porpoise Stocks working paper SOPS/79/36, 59 p.

[7]Cologne, J., and R. Holt. 1984. Observer effects in shipboard sight surveys of dolphin abundance. Southwest Fish. Cent. Adm. Rep. No. LJ-84-30, 42 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

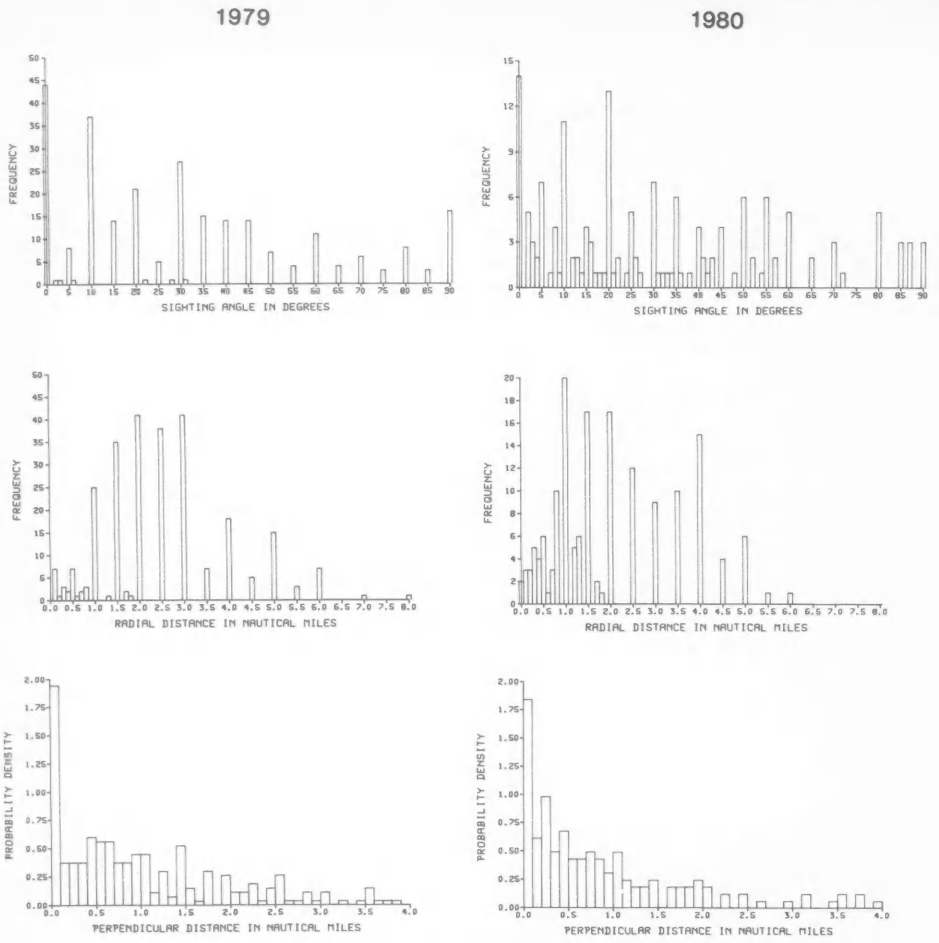

FIGURE 2.—Distribution of sighting angle, radial distance, and perpendicular distance from 1979, 1980,

With this system, the rounding to convenient values was not as evident (Fig. 2); however, measurements may still be inaccurate.

ANALYTICAL METHODS

Vessel data for area, sea state, sun glare, and observer performance strata were compared using rates of detection for all schools encountered within 2.13 km perpendicular distance of the ship (schools/1,000 km searched) and estimates of density of schools (schools/1,000 km^2). Similar comparisons of aerial data were completed using rates of detection for all schools encountered within 1.85 km perpendicular distance of the trackline, rates of detection for trackline schools, and estimates of school density.

Density estimates were made using line transect (LT) theory (Burnham et al. 1980). The basic equation (Seber 1973) is

$$D = \frac{n\,f(0)}{2L}$$

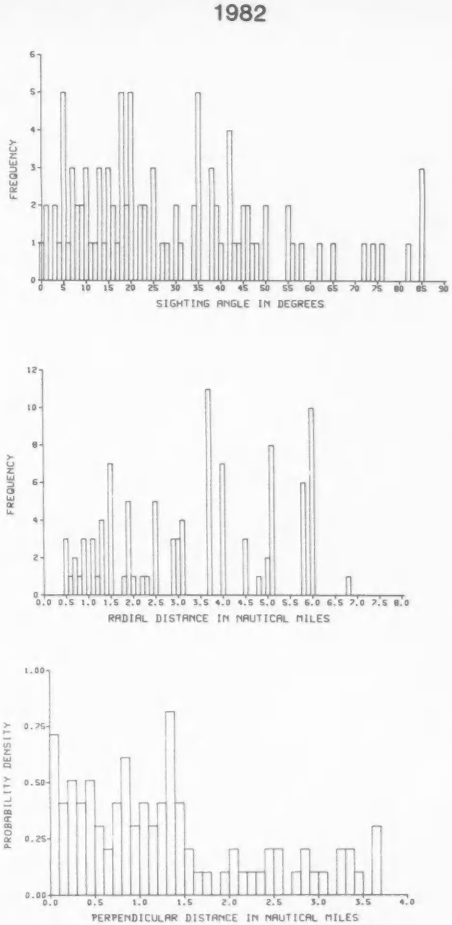

FIGURE 2.—*Continued*—and 1982 ship data.

where n is the number of schools sighted, D is the density of dolphin schools per km^2, L is the total linear distance searched (km), and $f(0)$ is a probability density function (*pdf*) evaluated at perpendicular distance, $x = 0$. The Fourier series (FS) model (Crain et al. 1979) was used to estimate $f(0)$ based upon criteria developed by Burnham et al. (1979). Burnham et al. (1980) is recommended for a full presentation of the FS model and for variance estimation.

Several assumptions must be met for valid use of LT theory. I investigated three of them for this study: 1) schools directly on the trackline are never missed, 2) schools do not move in response to the approaching ship or plane; and 3) no systematic measurement errors occur. All three assumptions have been made in analyzing previous aerial survey data (Holt and Powers 1982); however, field studies have subsequently been conducted to investigate the ability of observers to detect trackline schools (Holt 1983a), and whether or not dolphins avoid approaching ships (Au and Perryman 1982; Hewitt 1985). In addition, assumption 3 was not accepted because an inordinately large number of schools detected from the ships was recorded on the trackline.

Data Treatment

All species of dolphins encountered in the study area were included in the analyses. Of these, only schools with a mean minimum or mean best estimate of more than 14 animals were used because my field experience indicated that the probability that all animals in a school of at least this size would be submerged at one time, and hence undetectable, was very small. In addition, species affected by the fishery generally occur in schools with more than 14 animals.

During the first 18 of 20 flights of the 1979 aerial survey, two independent teams of three observers each searched for dolphin schools. Members of each team always searched for dolphins during the same time, alternating with the other team.

For aerial and 1979-83 ship data, observers recorded sea state conditions according to individual Beaufort, but during analyses, I grouped the data into 1) a "calm" sea state category: seas without whitecaps (Beaufort conditions 0-2) or 2) a "rough" sea category: seas with whitecaps (Beaufort conditions 3-5). Data for Beaufort conditions >5 were omitted from the analyses. The presence of whitecaps was important because animal splashes were used as sighting cues during calm conditions but could not be easily distinguished from whitecaps during rough conditions.

For aerial data and 1982-83 ship data, sun glare effects were investigated by classifying effort at various sun positions into "good" and "poor" categories depending on the amount of sun glare on the trackline (see Holt[8] for method used

[8]Holt, R. 1984. Testing the validity of line transect theory to estimate density of dolphin schools. Southwest Fish. Cent. Adm. Rep. No. LJ-84-31, 56 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

to record position of sun relative to the platform and for criteria used to define sun categories for aerial data). Criteria used for ship data were based upon observations recorded during a subsequent ship survey (Hohn[9]). Hohn found poor sun conditions on the trackline only when horizontal sun position was 12 and vertical position was 1, 2, or 3 or when clouds were accompanied by fog or rain. All other effort was defined as occurring during good conditions.

In order to apply the Fourier series (FS) model to aerial and ship data, I structured the data by 1) selecting appropriate interval widths for grouping the perpendicular sighting distributions (data cutpoints), 2) choosing a maximum observation distance perpendicular to the trackline (truncation point), 3) developing criteria to select the appropriate number of terms for the FS model, and 4) choosing the type of transformation to use in compensating for measurement error in the shipboard data.

Based on a subset of the ship data (Holt[10]), I used an interval width of 0.37 km (0.2 nmi) and truncated the perpendicular distance distributions at 3.7 km (2.0 nmi). Since perpendicular distance distributions for the ship data, and also to a lesser extent for aerial data, have very prominent modes or "spikes" at the origin, existing criteria to select the appropriate number of terms in the FS model were unsatisfactory. Therefore, I selected the model which provided the best visual fit to the distributions near the origin (Holt fn. 10). This technique was easily applied and was consistent among data sets. For use of the technique I assumed that the sizes of the spikes near the origins of the perpendicular distance distributions were indicative of relative density among the data sets. To minimize the effects of recording errors, the data were smoothed using the technique "smearing" (Butterworth 1982; Hammond 1984).

Based on previous investigations of aerial data (Holt and Powers 1982), I selected a truncation point of 1.94 km (1.05 nmi) and an interval width of 0.19 km (0.1 nmi) for the aerial data. I used the same technique as used for ship data to select the appropriate number of terms in the FS models; however, the aerial data were not smoothed because there was no evidence that the data contained estimation errors as did the ship data.

An estimate of density in the total area ($\hat{D}_c$) was calculated by combining the aerial inshore ($\hat{D}_i$) and ship offshore ($\hat{D}_0$) density estimates weighted by the relative sizes of the inshore (A_i) and offshore (A_0) areas as

$$\hat{D}_c = \frac{\hat{D}_i A_i + \hat{D}_0 A_0}{A_i + A_0}$$

The estimate of variance of $\hat{D}_c$ is

$$\hat{Var}(\hat{D}_c) = \frac{A_i^2 \hat{Var}(\hat{D}_i) + A_0^2 \hat{Var}(\hat{D}_0)}{(A_i + A_0)^2}$$

RESULTS

Factors Affecting Density Estimates

Aerial Data

Density estimates for the aerial data in the inshore area during calm seas or with minimal sun glare were more than twice the estimates for data taken during rough seas or poor sun conditions (Table 1). Differences in estimators were even greater for sea state and sun glare interaction effects. These differences may have occurred because observers failed to detect trackline schools during poor conditions or because sea state conditions were spatially confounded with distance from shore. Therefore, these differences may be reflecting a decreasing onshore-to-offshore density gradient. This was investigated by partitioning the inshore aerial data into "coastal" and "offshore" bands for each Beaufort sea state (Fig. 3) and sun glare condition (Fig. 4). Sufficient data were not available in each band to stratify detection rates by each sun and sea state interaction category.

Sea conditions during the aerial surveys were rougher offshore than nearshore. More searching was done in the coastal band during low Beaufort states, whereas more searching was done in the offshore band at higher Beaufort states (Fig. 3). The rates of detecting dolphin schools were higher at each corresponding Beaufort state in the coastal band than in the offshore band (Fig. 5). The rates of detecting trackline schools were generally higher in the coastal band; however, these rates were based upon very few

[9]A. Hohn, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. January 1985.

[10]Holt, R. 1984. Estimation of density of dolphin schools in the eastern tropical Pacific Ocean using line transect methods. Southwest Fish. Cent. Adm. Rep. No. LJ-84-32, 72 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 1.—Estimates of school density made during all conditions and during calm and rough seas using aerial and ship data; estimates made during good and poor sun condition using aerial data. Estimates are made for data in the inshore, offshore and total areas. Estimates for all conditions were calculated using 1977 through 1983 data and estimates for sun and sea state conditions were calculated using 1979 through 1983 data. Estimates are also presented for data collected during an aerial experiment testing effects of sea state and sun glare.

Variable	Distance searched (km)	Number schools detected (n)	Density ($\hat{D}$) (schools/ 1,000 km^2)	SE ($\hat{D}$)	CV ($\hat{D}$)
Inshore area					
Aerial data					
all data	34,006	152	4.18	0.902	0.216
calm seas	8,920	70	8.48	2.198	0.259
rough seas	25,086	82	2.71	0.611	0.255
good sun	11,994	74	6.57	1.504	0.229
poor sun	22,012	78	2.87	0.505	0.176
calm-good	3,026	30	12.64	5.290	0.418
calm-poor	5,894	40	6.24	2.311	0.370
rough-good	8,967	44	4.29	1.202	0.280
rough-poor	16,118	38	1.78	0.460	0.258
Ship data					
all data	27,840	379	4.47	0.514	0.115
calm seas	8,008	170	7.32	1.259	0.172
rough seas	14,668	149	4.05	0.772	0.191
Offshore area					
Ship data					
all data	46,567	322	2.04	0.263	0.129
calm seas	4,623	72	4.91	1.414	0.288
rough seas	20,976	99	2.01	0.435	0.217
All areas					
Ship data					
all data	74,407	626	2.95	0.253	0.086
calm seas	12,631	242	6.53	0.991	0.152
rough seas	35,644	248	3.02	0.445	0.147
Holt (text fn. 10) aerial experiment					
calm-good	1,414	37	29.18	7.357	0.252
calm-poor	3,014	81	23.78	5.888	0.248
rough-good	1,886	42	39.42	8.193	0.208
rough-poor	5,467	103	20.16	4.513	0.224

schools (18 trackline schools in the coastal and 10 schools in the offshore band were detected). Lower offshore estimates for data recorded under the same Beaufort state were consistent with a decreasing onshore-offshore density gradient.

Within each band, sea state conditions were also spatially stratified because the lower Beaufort conditions occurred mostly in the nearshore and northern regions of each band (Fig. 3). Predictably, detection rates for all schools within each band declined as the Beaufort condition increased. Because of the large variability inherent in small sample sizes and spatial stratification of searching effort at the various Beaufort conditions, comparisons of rates of detecting trackline schools did not yield consistent trends. For example, within both bands, the trackline detection rate for Beaufort 2 conditions was larger than for Beaufort 1 conditions. In the coastal band Beaufort 5 conditions had higher trackline detection rates than Beaufort 4 conditions and rates for Beaufort 4 were higher than rates for Beaufort 3 (Fig. 5).

Searching effort for aerial data during good and poor sun conditions was also confounded with distance from shore (Fig. 4) and thus with sea conditions. Most good sun conditions (78%) occurred in the coastal band, whereas 59% of all poor sun

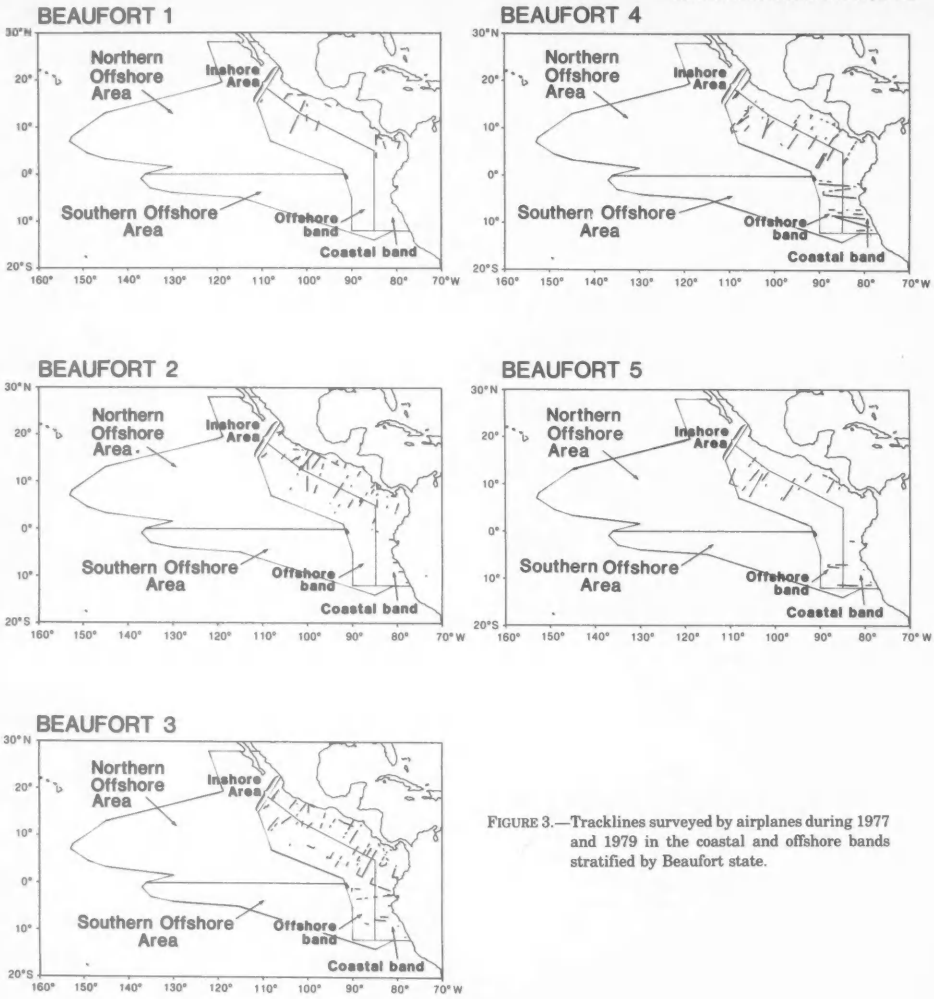

FIGURE 3.—Tracklines surveyed by airplanes during 1977 and 1979 in the coastal and offshore bands stratified by Beaufort state.

conditions occurred in the offshore band. This was because the general searching pattern was to begin searching on the westward, outbound leg in the morning, and then to turn the aircraft near noon and reach shore in late afternoon or night. Thus the sun was directly overhead or in front of the plane in the offshore reaches of the track and behind the plane in the nearshore areas.

Detection rates during good and poor sun conditions were higher in the coastal band than in the offshore band (Fig. 5), which was consistent with a hypothesized decreasing density gradient. Within the coastal band, detection rates during good sun conditions were greater than during poor sun conditions, but most of the poor sun data was gathered in the westward portion of the band (Fig. 4). In the offshore band, trackline detection rates during good and poor sun conditions were similar, but the rate during good sun conditions was based upon three sightings and only 8% of the effort.

Finally, I compared data collected by the ob-

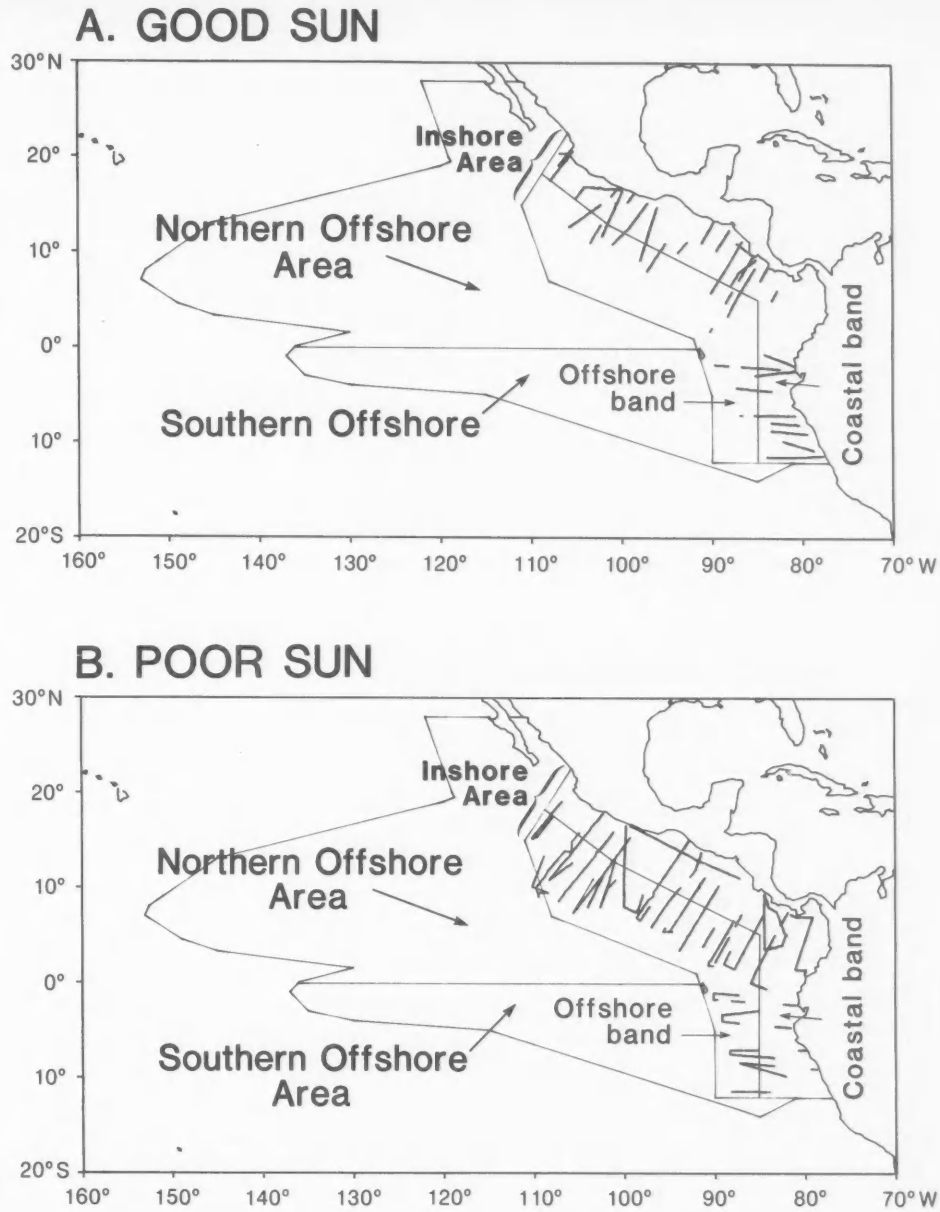

FIGURE 4.—Tracklines surveyed by airplanes during 1977 and 1979 during (A) good and (B) poor sun glare conditions in the coastal and offshore density bands.

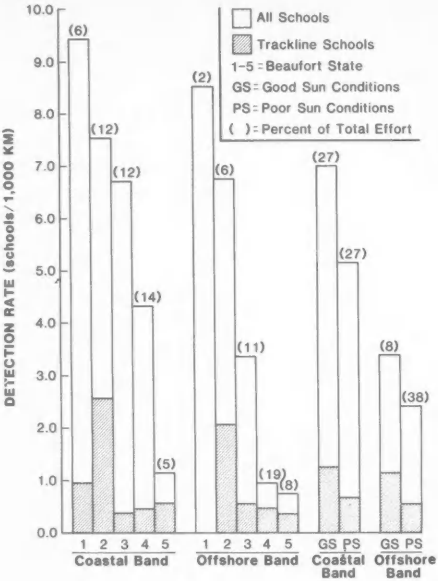

FIGURE 5.—School detection rates for aerial data in the coastal and offshore density bands for sea state and sun glare categories.

server teams to determine relative effects upon the density estimates. Team 1 and Team 2 searched approximately equal lengths of trackline (46% and 54% of the effort, respectively). No difference in performance of the two teams was evident: their rates of detecting schools, both on and off the trackline, and their estimates of school densities were approximately equal (Fig. 6).

Ship Data

The rates of detecting dolphins were greater during calm seas than during rough seas for the ship surveys from 1979 through 1983 (Fig. 7). The detection rate of dolphins during calm seas was more than twice the rate during rough seas in both the inshore and offshore areas. The ratio of calm sea to rough sea detection rates was larger in the offshore area than in the inshore area.

The offshore area was surveyed during rougher seas more than the inshore area (Fig. 8); seas were calm in the offshore area during only 17% of the effort as opposed to 35% for the inshore area surveys (Fig. 7). Dolphin density was lower offshore as indicated by lower offshore detection rates than inshore rates during either calm or rough seas (Fig. 7). The inshore-to-offshore-area detection ratios were 1.5 during calm seas and 2.0 during rough seas.

Sun glare had little effect on the shipboard estimates during either year because poor sun conditions occurred only during 6% of the 1982 and 8%

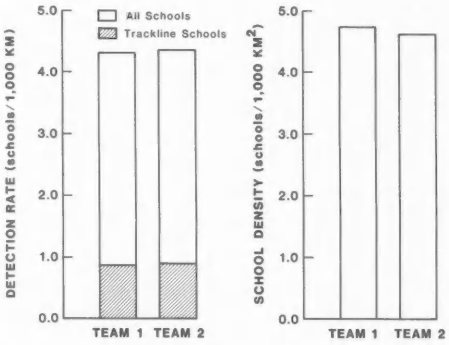

FIGURE 6.—School detection rates and density estimates for observer teams during the 1979 aerial survey.

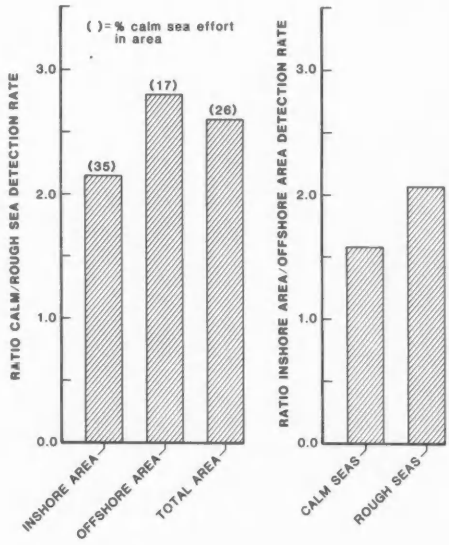

FIGURE 7.—Ratio of 1979-83 shipboard school detection rates for different sea states (calm sea versus rough sea) and area (inshore versus offshore). Detection rates computed with perpendicular distance data truncated at 2.1 km.

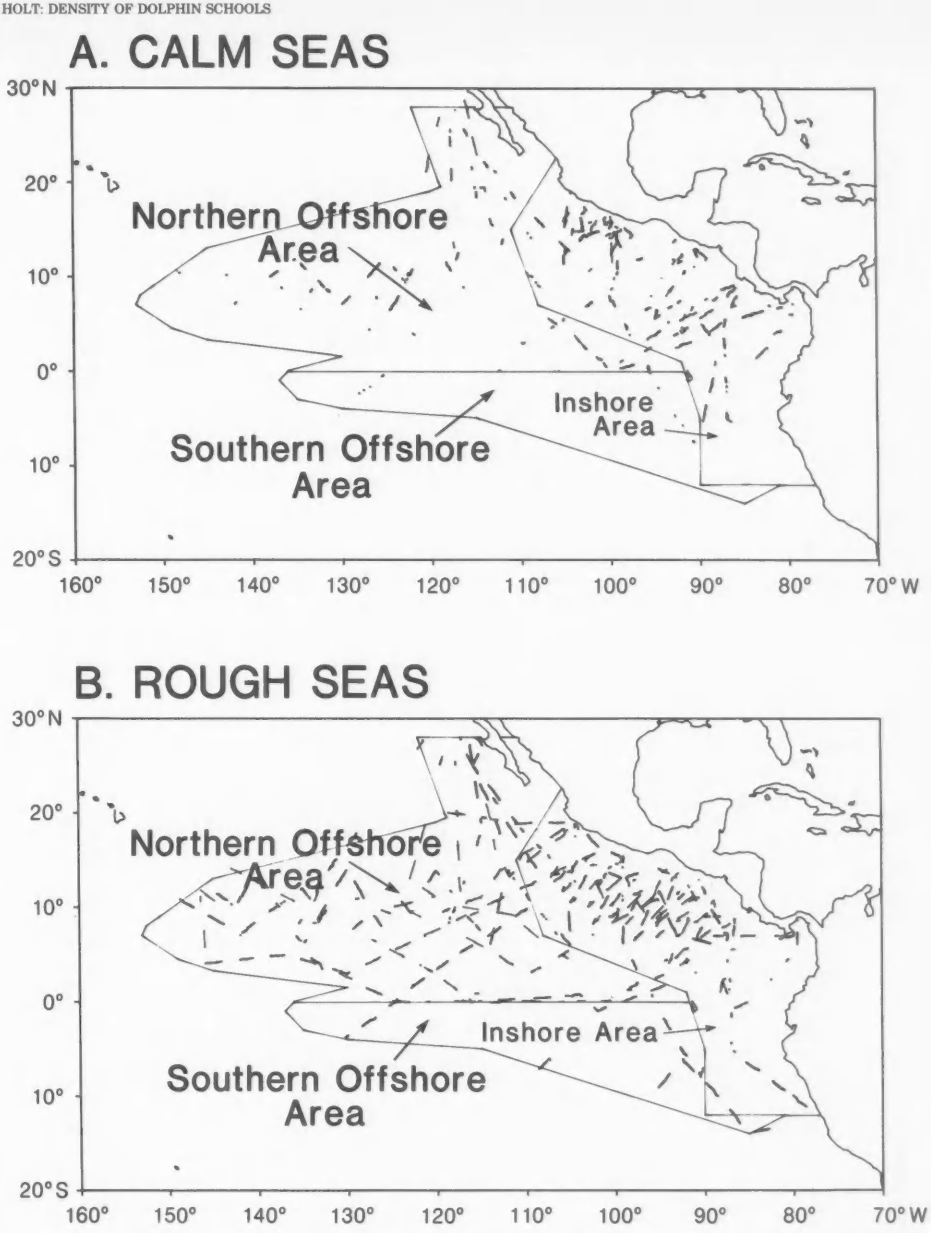

FIGURE 8.—Distribution of searching effort for the 1979-83 ship surveys during (A) calm and (B) rough conditions.

of the 1983 surveys. However, rates of detecting schools during good sun conditions were larger than during poor conditions (Fig. 9) and no schools were detected on the trackline during poor conditions.

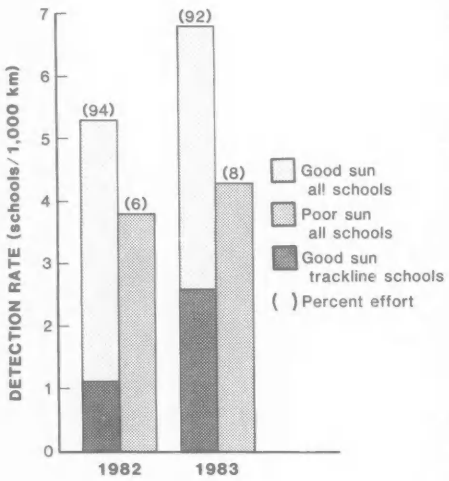

FIGURE 9.—School detection rates and relative density estimates during good and poor sun glare conditions for 1982 and 1983 ship data.

Density Estimates

Inshore Area

Aerial observers during the 1977 and 1979 surveys searched 34,006 km and detected 152 dolphin schools in the inshore area (Table 1). The estimate of school density using aerial data was 4.18 schools/1,000 km^2 with a standard error of 0.902.

From 1977 to 1983, shipboard observers searched 27,840 km in the inshore area and detected 297 schools (Table 2). Ship data yielded an estimate of density for the inshore area of 4.47 schools/1,000 km^2 with a standard error of 0.514 (Table 1). This was only slightly larger than the aerial inshore estimate.

Offshore Area

Observers aboard both vessels surveyed 46,567 km in the offshore area and detected 192 schools (Table 2). The estimate of density was 2.04 schools/1,000 km^2 with a standard error of 0.263 (Table 1).

Total Area

From 1977 to 1983, observers on both vessels searched 74,407 km in all areas and detected 489 schools (Table 2). The density estimate for all shipboard data was 2.95 schools/1,000 km^2 with a standard error of 0.253 (Table 1). The estimate of density using the aerial inshore estimate and the

TABLE 2.—School detection rates for 1977-83 ship data and for 1979-83 ship data stratified by sea state category in the inshore, offshore and total areas. Data were truncated at 2.13 km perpendicular distance.

Area/data source	Distance searched (km)	Percent (km) searched	Number schools detected	Percent schools detected	Detection rate (schools/ 1,000 km)	SE (detection rate)	Number days searched
Inshore area							
77-83 all data	27,840	100.0	297	100.0	10.67	0.82	173
79-83 calm seas	8,502	35.3	144	53.9	16.94	1.52	89
79-83 rough seas	15,609	64.7	123	46.1	7.88	0.92	124
Offshore area							
77-83 all data	46,567	100.0	192	100.0	4.12	0.50	251
79-83 calm seas	4,129	17.1	44	36.7	10.66	2.30	58
79-83 rough seas	20,015	82.9	76	63.3	3.80	0.56	134
Total area							
77-83 all data	74,407	100.0	489	100.0	6.57	0.47	417
79-83 calm seas	12,632	26.2	188	48.6	14.88	1.29	146
79-83 rough seas	35,624	73.8	199	51.4	5.59	0.54	256

ship offshore estimate was 2.71 schools/1,000 km^2 with a standard error of 0.334.

DISCUSSION

Onshore-Offshore Density Gradients

The onshore-to-offshore density gradient decreased based on aerial data in the inshore area and comparison of inshore and offshore density estimates. Offshore density estimates were only about one-half the inshore estimates (Table 1). Although sea state and sun glare conditions were confounded with distance from shore, comparisons of detection rates in the two inshore density bands for data stratified by Beaufort state or sun conditions indicated lower rates in the outer band (Fig. 5).

Fit of Fourier Series Model

Burnham et al. (1980) provided criteria for selecting the appropriate number of terms in the FS model. However, these criteria were not satisfactory for use with the aerial and ship perpendicular distance distributions, which had pronounced modes at the origin. Instead, I selected models which had the fewest terms but provided a good fit near the origin. This resulted in models with large numbers of terms. However, to the degree that the modes are representative of school density, my estimates of densities will be unbiased. Alternate statistical models need development which can fit data which lack a shoulder near the origin (i.e., data with pronounced modes at the origin). Buckland (1985) investigated several models but concluded that reliable estimation is not possible unless a shoulder exists.

Line Transect Assumptions

Aerial Data

Confounding of aerial sea state and sun condition data with distance from shore made it impossible to test the assumption that all trackline schools were detected during all viewing conditions. If viewing conditions had been homogeneous throughout the area, the density estimate calculated for calm sea and good sun conditions (12.64 schools/1,000 km^2) could be used for the inshore area (Table 1). This estimate is over 7 times the rough sea and poor sun estimate (1.78 schools/1,000 km^2). However, the calm seas and good sun condition effort occurred mostly in the northern nearshore region of the inshore area (Fig. 3, 4) where density may be high.

Consequently, Holt (fn. 8) conducted an aerial experiment in a relatively small area to test sea state and sun effects upon LT density estimates. The results indicated that sun glare adversely affected estimates of school density. The density estimate was 39% larger during good sun conditions than during poor conditions. Although density estimates were larger for calm sea data than for rough sea data, the differences were not significant.

The aerial experimental data (Holt fn. 8) may be used to estimate maximum bias for sun and sea state effects. The adjusted density estimate ($\hat{D}_A$) is

$$\hat{D}_A = \sum_{i=1}^{2}\sum_{j=1}^{2} \hat{D}_{ij} P_{ij} \left(\frac{\hat{D}'_{11}}{\hat{D}'_{ij}}\right)$$

where $\hat{D}_{ij}$ = Density estimate in survey area during ith sea state and jth sun condition,

P_{ij} = Proportion of effort in survey area with ith sea state and jth sun condition,

D'_{ij} = Experimental density estimate during ith sea state and jth sun condition determined from Holt (fn. 8).

In addition, i equal 1 denotes calm sea states and i equal 2 denotes rough sea states, and j equal 1 denotes good sun conditions and j equal 2 denotes poor sun conditions. An estimate of the sampling variance ($\mathrm{Var}(\hat{D}_A)$) using the Taylor approximation method is

$$\hat{Var}(\hat{D}_A) = \sum_{i=1}^{2}\sum_{j=1}^{2} P_{ij}^2 \left[\left(\frac{\hat{D}_{ij}}{\hat{D}'_{ij}}\right)^2 \hat{Var}(\hat{D}'_{11}) + \left(\frac{D'_{11}}{D'_{ij}}\right)^2 \hat{Var}(\hat{D}_{ij}) + \left(\frac{\hat{D}_{ij}\hat{D}'_{11}}{(\hat{D}'_{ij})^2}\right)^2 \hat{Var}(\hat{D}'_{ij}) \right].$$

The adjusted inshore density estimate is 4.51 schools/1,000 km^2 with a standard error of 1.107. This is an 8% increase over the unadjusted esti-

mate (Table 1). The adjusted combined estimate for the entire ETP was 2.81 schools/1,000 km^2 with a standard error of 0.152, a 4% increase from the unadjusted estimate.

Using the experimental results to adjust aerial estimates for sun glare (and possibly sea state), effects may be suspect because of differences in procedures followed and observational conditions encountered in the experiment and the surveys: 1) The wings on the aircraft used during the experiment were attached on the lower part of the fuselage, whereas wings on the 1977 and 1979 aircraft were attached to the upper part of the craft which allowed better lateral observation. 2) Procedures used to adjust for presence of sun glare during the surveys and the experiment differed. Observers during the surveys were instructed to stop searching if they believed conditions prevented their detecting trackline schools, but observers in the experiment searched during all conditions. 3) More rough seas were encountered during the surveys (74%) than in the experiment (62%). Also, more (46% as compared to 15%) of the surveys' total effort occurred at extreme Beaufort 4 and 5 conditions. Because of these uncertainties, I used the unadjusted density estimate to determine school densities.

Comparisons of the 1979 aerial observer teams' estimates did not indicate observers of either team missed dolphin schools on the trackline but both teams may have been equally affected by searching conditions. These results were consistent with results of the aerial experiment (Holt fn. 8) where comparisons of observer teams' performance also indicated no significant differences.

Ship Data

The density estimates calculated from calm sea data were larger than estimates calculated from rough sea data (Table 1). The difference was probably not due to missed trackline schools during rough seas. Schools on the trackline would probably be detected as the ship approached unless the schools avoided the approaching ship. In a ship-helicopter experiment Hewitt (1985) investigated the reaction of dolphins to survey vessels and found that dolphin schools only occasionally react to the approach of a vessel before they are detected by shipboard observers (1 of 12 schools).

The differences between calm and rough sea estimates may have resulted from actual differences in densities in areas surveyed during calm and rough sea states (Fig. 8). Another possibility is that estimation errors resulted from observers detecting schools at greater radial distances during calm conditions (mean radial distance was 4.16 km) than during rough conditions (mean radial distance was 3.55 km). Estimation of sighting angles and distances of schools at greater distances from the ship may have been less accurate and may have increased the probability of schools being erroneously recorded near or on the trackline.

Although sun glare was not shown to affect the shipboard density estimates, Cologne and Holt (fn. 7) found that shipboard observers tended to avoid searching areas with sun glare. However, because of the relatively slow speed of the ship and the dolphins and because sun glare at any specific time is usually concentrated in a small region of the observers' field of view, all regions may be observed without glare.

The occurrence of errors in angle and distance estimations may have positively biased shipboard estimates. An inordinate proportion of dolphin schools (25% of all schools) was recorded as being on the trackline. Smearing the perpendicular distance distributions helped alleviate the bias but may not have eliminated it.

Comparison of Aerial and Ship Estimates

The estimates of dolphin densities in the inshore and the total areas using only ship data were slightly larger than estimates which used aerial inshore data (Table 1). This is logical because ship surveys were designed to overlap with aerial coverage in the inshore area and to provide systematic coverage of the offshore area. Therefore, they spent disproportionately more of their effort in the inshore area compared to its relative size and, within the inshore area, they spent disproportionately more effort in the northern nearshore region (Fig. 1), which has relatively high dolphin density. Although the inshore area represented 31% of the total area, 37% of the ship's effort was in the inshore area. In addition, 61% of the inshore effort was in the northern inshore region which represented approximately 44% of the inshore area. During the aerial surveys a systematic survey of the inshore area was conducted. Therefore, the best estimates of densities in the inshore and total areas are estimates calculated using the unadjusted aerial inshore data.

Comparisons with Previous Density Estimates

Density of ETP dolphin stocks have been estimated previously (SWFC 1976[11]; Holt and Powers 1982). The methods I used to calculate estimates were similar to those used by Holt and Powers. Therefore, differences that they noted between their assessment in 1979 and the SWFC 1976 assessment are also applicable to comparisons between the SWFC 1976 assessment and this study. My estimates differ from the 1979 estimates in that mine include

1) schools where either the observers' "best" or "lowest" estimate of mean school size was more than 14 animals (the 1979 assessment included only schools with "best" estimates),
2) use of the 1977 aerial data in the inshore density estimate,
3) ship data collected in 1977, 1979, 1980, 1982, and 1983 (the 1979 assessment included only 1979 ship data),
4) investigation of aerial and ship data for effects of sun, sea state, and observer performance,
5) application of LT methods to ship data to calculate density estimates.

Density estimates calculated in this study were similar to those presented in the 1979 assessment (Holt and Powers 1982). My inshore and offshore estimates were 4.18 and 2.04 schools/1,000 km^2, respectively, with standard errors of 0.902 and 0.263. Holt and Power's estimates were 3.51 and 1.89 schools/1,000 km^2, respectively, with standard errors of 0.590 and 0.766.

CONCLUSIONS

LT methods were used on 1977 and 1979 aerial survey data to estimate dolphin density in the inshore area at 4.18 schools/1,000 km^2. LT methods applied to 1977-83 ship data yielded an estimate of offshore dolphin density of 2.04 schools/1,000 km^2. By weighting aerial inshore and ship offshore data by the respective size of the two areas, the total dolphin density was estimated at 2.71 schools/1,000 km^2.

I investigated differences among densities at different visibility conditions for aerial data, but results were inconclusive owing to confounding of the factors with density gradient (area from shore). Adjusting the data for sea state and sun conditions increased the inshore aerial density estimate 8% and the total density estimate by 4%.

ACKNOWLEDGMENTS

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RESEARCH VESSEL SURVEY DESIGN FOR MONITORING DOLPHIN ABUNDANCE IN THE EASTERN TROPICAL PACIFIC

RENNIE S. HOLT,[1] TIM GERRODETTE,[2] AND JOHN B. COLOGNE[3]

ABSTRACT

During 1986 the National Marine Fisheries Service began conducting long-term research ship surveys to determine status of spotted dolphin, *Stenella attenuata*, stocks in the eastern tropical Pacific. This is the main dolphin species taken incidentally by the yellowfin tuna, *Thunnus albacares*, purse seine fishery. We use research vessel survey data collected from 1977 to 1983 to investigate the annual changes in spotted dolphin population size that could be detected given various levels of research vessel survey effort during specified time periods for several levels of statistical error.

We find that two research vessels each operating for 120 days per year for 5 years (six surveys) could detect a 10% annual rate of decrease in dolphin abundance (a total 41% decrease over 5 years) with alpha and beta error levels of 10%. Adding a third vessel would provide better coverage of the dolphins' range, but would allow only a slightly lower rate of decrease to be detected (an 11% annual rate, for a total decrease of 44%). These numbers point out the difficulty of detecting even major changes in spotted dolphin population size with present survey methods. Alternatives are discussed, but all either cost more money, require a longer time to detect a decline, or accept higher levels of statistical error.

The National Marine Fisheries Service (NMFS) has the responsibility of determining the status of dolphin stocks which are taken incidentally by the yellowfin tuna, *Thunnus albacares*, purse seine fishery in the eastern tropical Pacific (ETP) (Richey 1976[4]). The status of spotted dolphins, *Stenella attenuata*, is of special concern since it is the major species taken by the fishery (Smith 1979[5]). Of the spotted dolphins, the northern offshore stock is of more concern since it has been fished more frequently than the southern offshore stock. The spinner dolphin, *S. longirostris*, and the common dolphin, *Delphinus delphis*, are also taken. In addition, the striped dolphin, *S. coeruleoalba*, and the Fraser's dolphin, *Lagenodelphis hosei*, are occasionally caught but are difficult to distinguish from the other three species at a distance (Holt and Powers 1982). These 5 species are herein termed target species.

The NMFS conducted assessments of population status in 1976 (SWFC 1976[6]) and again in 1979 (Smith fn. 5) based on estimates of *absolute* stock abundance. The validity of the absolute estimates depended on several assumptions being met. Unfortunately, some assumptions, such as not allowing systematic errors in data recording or the assumption that dolphin schools do not move prior to being detected by shipboard observers, may not have been met and thus the assessments were not entirely satisfactory. An alternative approach for assessing stock status, therefore, is to use *relative* population estimates to detect trends in stock sizes over a long time period. Relative estimates can provide an assessment of stock condition as long as the biases in the abundance estimates are consistent over the sampling period. Therefore, the NMFS is presently considering using annual estimates of population abundance as relative estimates to detect declines in population size of spotted dolphins during a sampling period of at least 5 years.

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In this paper, we investigate the annual changes in the size of spotted dolphin populations that can be detected given various levels of research vessel survey effort within specified time periods. We investigate how many research vessels, assuming 120 days searching per vessel per year, would be required to survey the physical area inhabited by the major stocks. We also investigate how many vessels would be required to detect various levels of population declines in spotted dolphins during 5 years or, given fixed number of vessels, how many years of survey effort it would take to detect various population declines or, given fixed number of vessels for fixed number of years, the probability of detecting a decline (i.e., the power). We use historical data and current abundance techniques to predict variability of data which will be collected during the sampling period.

AREA INHABITED AND DATA SOURCES

For our analyses, the study area included the area described by Au et al. (1979)[7] as being inhabited by the target species (Fig. 1). The area north of lat. 20°N was excluded because spotted dolphins do not usually occur there. We partitioned the study area into four strata: the inside, middle, and west strata, which are located north of lat. 1°S, and a south stratum. The three northern strata were collectively termed the north area and all strata were termed the total area. In addition, a calibration area was defined as including part of the inside stratum (Fig. 1).

Data used in our analyses were collected from 1977 through 1983 by scientific observers aboard the NOAA ships *David Starr Jordan* and *Townsend Cromwell*. Survey coverage from the two ships for all years combined was thorough (Fig. 1). Data collected for each school included estimates of dolphin school size, species composition, and line transect observations, which we used to calculate density estimates.

SURVEY COVERAGE

We investigated the physical coverage of the area that is possible when using 1, 2, or 3 ships for

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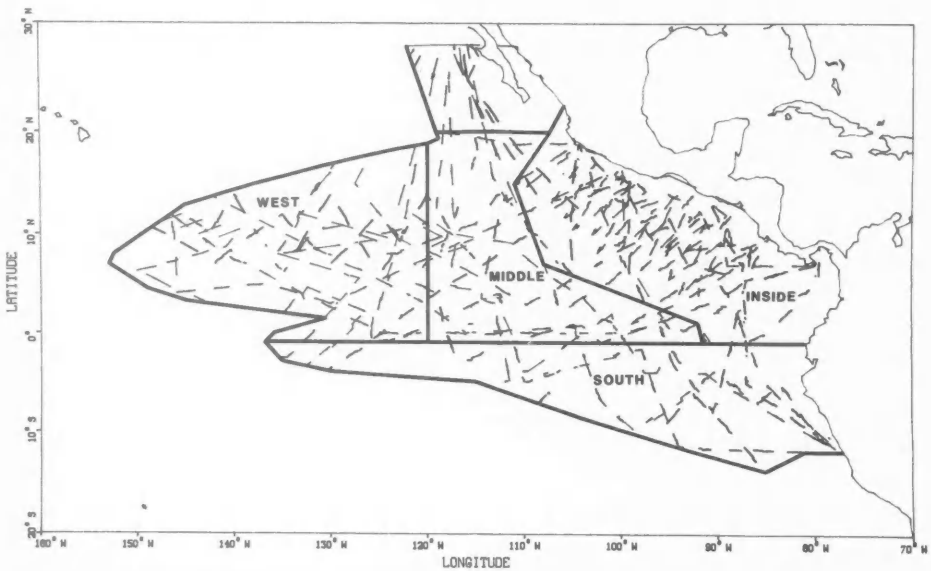


FIGURE 1.—Research vessel tracklines in each stratum during 1977 through 1983.

120 days each by plotting hypothetical tracklines. Approximately 370 km (200 nautical miles) of trackline could be covered in each survey day; with searching restricted to daylight hours, only about one-half of this distance would be searched. Approximately 40,700 km of trackline could be covered by each ship with less than 50% of this distance searched during daylight hours. Each ship's searching distance was allocated to each stratum by the square root of school density in the stratum. Effort of each ship was partitioned into 30-d segments between ports to meet logistical constraints of the vessels. We found that thorough coverage of the entire area was provided when three ships were used, two ships provided adequate coverage, and one ship provided very poor coverage with tracklines separated by large distances (Fig. 2).

DETECTION OF CHANGES IN POPULATION SIZE

Survey Design

The relationship among the number of samples, the rate of change, the precision of the population estimate, and the levels of alpha (type I) and beta (type II) statistical errors for several models of change and sample variability was investigated by Gerrodette (in press). We assumed that population size would change exponentially (constant rate per year). From Gerrodette's equation 15, using slightly different notation,

$$a(a+1)^2(a+2)[\ln(1-r)]^2 \geq 12(Z_\alpha + Z_\beta)^2 \sum_{i=0}^{a} \ln\left[\frac{CV_0^2}{(1-r)^i} + 1\right] \qquad (1)$$

where a = number of years in the survey period,
r = annual rate of decrease,
Z_α = percentile of standardized normal curve for one-tailed Type I error,
Z_β = percentile of standardized normal curve for Type II error, and
CV_0 = coefficient of variation of the population estimate at the present population size.

In this formulation, r is a positive number, and, since the first survey occurs at time 0, the total number of samples (i.e., number of annual surveys) is $a + 1$. Note that the null hypothesis is one-sided, namely, that spotted dolphin abundance is decreasing. In addition to the annual rate of decrease (r), the total population decrease which would occur over the entire survey period was calculated as

$$\text{Total decrease} = [1 - (1 - r)^a].$$

The survey design to detect changes in dolphin abundance was investigated in three ways. Using Equation (1), we computed 1) the minimum number of years (a), given one to three ships per year and 120 searching days per ship per year, required to detect various annual decreases in spotted dolphin abundance; 2) the minimum proportional annual change (r) that could be detected in 5 years given one to three ships per year at various levels of alpha and beta; and 3) power ($1 - \beta$) or the probability of detecting various decreases in population size in 5 years, given one to three ships per year.

To use Equation (1), the relationship of $CV(\hat{N})$, the coefficient of variation of the population estimate, and n, the number of schools detected must be determined. In addition, the rate per day at which dolphin schools are expected to be encountered must be known. We used the 1977–83 research vessel data to investigate these factors assuming these data would be representative of data that we will obtain during the proposed sampling period of 1986–91.

Abundance Estimation

Relative estimates of population abundance of spotted dolphins in the north and total areas were calculated using two methods, methods A and B. In method A, density and mean school size estimates were calculated in each stratum and abundance was determined (Holt and Powers 1982) as

$$\hat{N} = \hat{P}_t \sum_{k=1}^{m} \hat{D}_k \hat{S}_{tk} \hat{P}_k A_k. \qquad (2)$$

In method B, density and mean school size estimates were calculated for data pooled for the entire area (north area or total area) and abundance was determined as

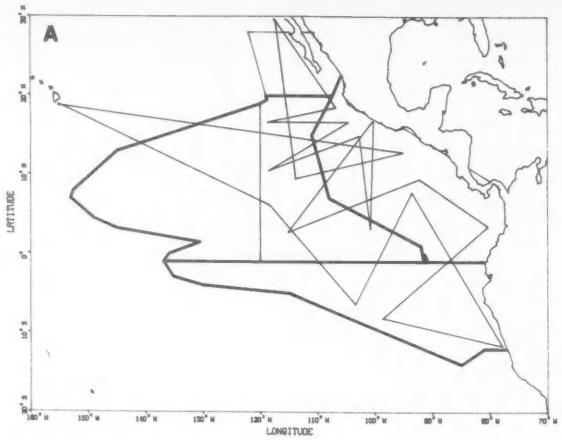


FIGURE 2.—Plot of hypothetical tracklines expected from use of one (A), two (B), or three (C) ships for 120 days each.

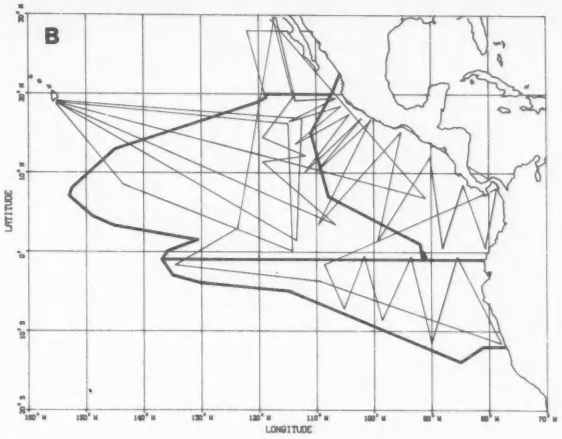
$$\hat{N} = \hat{P}_t \hat{D} \hat{S} \sum_{k=1}^{m} \hat{P}_k A_k. \quad (3)$$

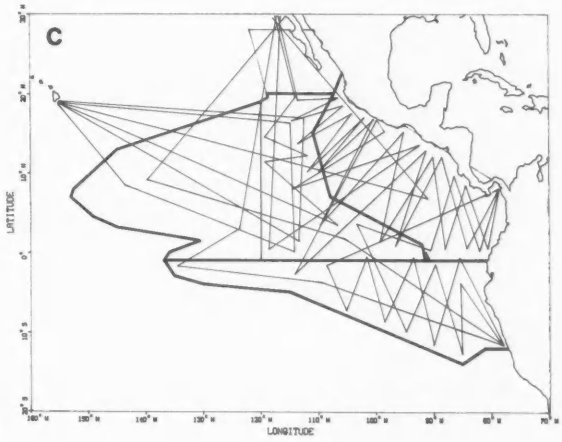
where m = number of strata (3 for the north area and 4 for the total area),
k = 1, 2, 3, or 4 denotes the inside, middle, west, or south stratum, respectively,
$\hat{N}$ = estimated number of spotted dolphins in the survey area,
$\hat{D}$ = density estimate of number of schools of all dolphin species in the survey area (schools/1,000 km^2),
$\hat{D}_k$ = density estimate of number of schools of all dolphin species in the kth stratum (schools/1,000 km^2),
$\hat{S}$ = mean school size estimate for target species in the survey area (number of animals),
$\hat{S}_{tk}$ = mean school size estimate for target species in the kth stratum (number of animals),
$\hat{P}_t$ = proportion of all dolphins that were target species in the survey area,
$\hat{P}_k$ = proportion of spotted dolphins in the target schools in the kth stratum, and
A_k = area inhabited by all dolphins in the kth stratum.

The variance of $\hat{N}$ for Equation (2) was estimated using Taylor series expansion (Seber 1973) as

$$\begin{aligned} \text{Vâr}(\hat{N}) = \sum_{k=1}^{m} [&(\hat{S}_{tk} \hat{P}_t \hat{P}_k A_k)^2 \text{ Vâr}(\hat{D}_k) \\ &+ (\hat{D}_k \hat{P}_t \hat{P}_k A_k)^2 \text{ Vâr}(\hat{S}_{tk}) \\ &+ (\hat{D}_k \hat{S}_{tk} \hat{P}_k A_k)^2 \text{ Vâr}(\hat{P}_t) \\ &+ (\hat{D}_k \hat{S}_{tk} \hat{P}_t A_k)^2 \text{ Vâr}(\hat{P}_k)] \; . \end{aligned} \quad (4)$$

The variance of $\hat{N}$ in Equation (3) was determined using Equation (4), but density and school size estimates that were calculated for the entire area





were substituted for the respective stratified estimates.

Specific formulae to estimate variables and associated theoretical variances in Equations (2) through (4) are from Burnham et al. (1980), Holt (1985,[8] in press) and Barlow and Holt (1986). Variances for estimates of school sizes and school densities were calculated using jackknife techniques (Miller 1974).

Since serial correlation among sampling units (days of effort) will yield biased estimates of standard errors using the jackknife method, we analyzed serial correlation of dolphin school detection rates among various combinations of successive days of effort. Analyses indicated that correlation was significant among successive single days but was not significant for periods of 2 or more days. Therefore, the data were grouped by 2-d increments for the jackknife analyses.

Estimates of spotted dolphin population abundance and values used in Equations (2) and (3) to calculate the estimates are presented in Table 1. CV ($\hat{N}$)s were smaller for estimates calculated using method B than for estimates using method A.

[8]Holt, R. S. 1985. Estimates of abundance of dolphin stocks taken incidentally in the eastern tropical Pacific yellowfin tuna fishery. Southwest Fish. Cent. Adm. Rep. No. LJ-85-20, 32 p. SWFC La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 1.—School density of all dolphin schools, proportion of all schools which were target schools, mean school size of target schools, proportion of target animals which were spotted dolphins, area of each stratum, abundance and K values for spotted dolphins. SE and CV denote standard error and coefficient of variation, respectively. Methods A and B refer to different ways of pooling data on school size and density (see text).

Variable	Stratum				Area	
	Inside	Middle	West	South	North	Total
School density ($\hat{D}$) (Schools/1,000 km^2)	5.33	3.42	0.82	1.93	3.20	3.03
SE ($\hat{D}$)	0.87	1.13	0.30	0.39	0.54	0.51
CV($\hat{D}$)	16.3	33.1	37.2	20.2	17.0	16.8
Prop. target (P_t)[1]	—	—	—	—	0.775	0.775
Mean school size (S_t) (Number animals)	108.59	113.89	121.06	157.65	111.62	118.21
SE (S_t)	9.82	11.24	23.28	29.84	7.44	7.92
CV (S_t)	8.6	9.9	19.2	18.9	6.7	6.7
Area (km^2 * 10^6)	4.602	3.764	5.298	4.359	13.664	18.024
Prop. spotted (P_k)[2]	0.38	0.51	0.51	0.26	—	—
SE (P_k)[2]	0.039	0.048	0.048	0.085	—	—
Abundance and K Values						
Method A						
$\hat{N}$ (Animals * 10^6)					1.571	1.839
SE ($\hat{N}$)					0.283	0.294
CV ($\hat{N}$)					0.18	0.16
Sample size (n)					507	602
K					4.05	3.93
Method B						
$\hat{N}$ (Animals * 10^6)					1.761	2.081
SE ($\hat{N}$)					0.240	0.250
CV ($\hat{N}$)					0.14	0.12
Sample size (n)					507	602
K					3.06	2.94

[1]Source Holt (in press).
[2]Source Barlow and Holt (1986).

Relationship Between Var ($\hat{N}$) and Number of Schools Detected

In order to minimize the number of years required to detect a specific trend, Var ($\hat{N}$) should be as small as possible (Gerrodette in press). Var ($\hat{N}$) depends on the variance of the estimates of school size, school density, and proportions of the various dolphin species, as shown in Equation (4). Each of the variances of these estimates, in turn, depends on n, the number of sighted schools. Therefore, the dependence of Var ($\hat{N}$) on n must be known to calculate the number of sightings needed to attain a given level of precision (Var ($\hat{N}$)). We investigated the dependence of each of the individual variance terms on n.

Dependence of Var (S_{tk}), Var ($\hat{P}_t$), and Var ($\hat{P}_k$) on n

Because $\hat{S}_{tk}$ is the mean of n individual school size estimates, its variance is Var ($\hat{S}_{tk}$) = Var (S_{tk})/n where Var (S_{tk}) is the variance of school size. The Var ($\hat{P}_t$) = $P_t(1 - P_t)/n$ where P_t is the true proportion of target schools among all dolphins. Var (S_{tk}) and $P_t(1 - P_t)$ are both constant with respect to n, so Var ($\hat{S}_t$) = $O(1/n)$ and Var ($\hat{P}_t$) = $O(1/n)$, where $O(1/n)$ means "of the same order as $1/n$" and implies that as $1/n$ approaches zero, the variance approaches zero at the same rate. Similarly, Var ($\hat{P}_{ik}$), which is also a proportion, is equal to $O(1/n)$.

Dependence of Vâr ($\hat{D}$) on n

The Vâr ($\hat{D}$), based on replicate tracklines (Burnham et al. 1980), is

$$\text{Vâr}(\hat{D}) = \hat{D}^2 \left[\frac{\text{Vâr}(n)}{n^2} + \frac{\text{Vâr}[\hat{f}(0)]}{[\hat{f}(0)]^2} \right] \quad (5)$$

where n is the number of sightings and $\hat{f}(0)$ is the

estimate of the probability density function of perpendicular distances extrapolated to the trackline. First,

$$\text{Vâr}\,(n) = \frac{R\sum_{i=1}^{R}(n_i - \bar{n})^2}{R-1}$$

where R is the number of replicate lines of equal length (l). For R of moderate size, $R \cong (R-1)$. Thus

$$\text{Vâr}\,(n) = \sum_{i=1}^{R}(n_i - \bar{n})^2 = O(\text{R}).$$

This is because Vâr (n) is the sum of the variances of R independent values (n_i, $i = 1, 2, \ldots, R$) each having the same expected variance. But $R = n/E(n_1)$, the total number of sightings divided by the expected number of sightings for a line of length l. Thus, $R = O(n)$, and

$$\frac{\text{Vâr}\,(n)}{n^2} = \frac{O(n)}{n^2} = O(1/n). \qquad (6)$$

Second, $\hat{f}(0)$ was estimated using a Fourier series (FS) model (Burnham et al. 1980); therefore,

$$\text{Vâr}\,[\hat{f}(0)] = \sum_{j=1}^{m}\sum_{k=1}^{m}\text{Cov}\,(\hat{a}_j, \hat{a}_k)$$

$$k = 1, 2, 3, \ldots, \textit{and}\ k > j > 1$$

where the a's are the coefficients in the series

$$\hat{a}_k = \frac{2}{nw}\left[\sum_{i=1}^{n}\cos\left(\frac{k\pi x_i}{w}\right)\right] = O\,(1)$$

with x_i equal the perpendicular distance to the ith sighting and w equal the truncation point for the perpendicular distance. Therefore, we only need to know the dependence of cov(a_j, a_k) on n. If n is much larger than one, $(n-1) \cong n$ and

$$\text{Côv}\,(\hat{a}_j, \hat{a}_k) = \frac{1}{n-1}\left[\frac{1}{w}(\hat{a}_{k+j} + \hat{a}_{k-j}) - \hat{a}_j\,\hat{a}_k\right]$$

$$= O\,(1/n).$$

Since $\hat{f}(0)$ estimates a quantity which is constant with respect to n,

$$\frac{\text{Vâr}\,[\hat{f}(0)]}{[\hat{f}(0)]^2} = O\,(1/n). \qquad (7)$$

Combining Equations (6) and (7) with Equation (5), $[\text{CV}\,(\hat{D})]^2 = O(1/n)$. This confirms discussions presented by Burnham et al. (1980).

In addition to investigating the theoretical dependence of $[\text{CV}\,(\hat{D})]^2$ on n, we tested its empirical dependence on n using the research vessel data which included 479 days of survey effort. Data were truncated at 3.70 km perpendicular distance from the ship. Paired days of shipboard searching effort were randomly selected using a uniform random number generator until the number of associated sightings (n) equaled or exceeded a previously selected sample size. Sample sizes selected were 20, 30, 40, 50, 60, 80, 100, 200, 500, and 1,000. The resultant perpendicular distance distributions were smeared (a data smoothing technique described by Butterworth 1982, Hammond 1984, and Holt fn.8), and density, variance, and coefficient of variation estimates were calculated for each data set. The simulation was completed three times for each value of n.

The relationship between CV $(\hat{D})$ and $1/\sqrt{n}$ (Fig. 3) was linear ($F_{\text{lack-of-fit}} = 0.83$; $P = 0.59$) with intercept not significantly greater than zero ($t = 1.56$; $P > 0.10$). This confirms the analytical result above, that $\text{CV}\,(\hat{D}) = O(1/\sqrt{n})$; however, as n increased, the probability of randomly selecting data from each of the 240 pairs of days (479 survey days) multiple times increased which may

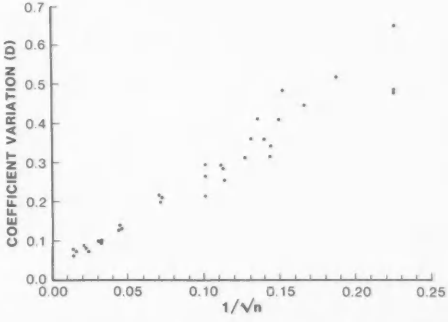


FIGURE 3.—Comparison of number of dolphin sightings ($1/\sqrt{n}$) and precision of the population estimate (CV(D)).

have biased CV ($\hat{D}$) if the distribution of sightings for the days were biased due to the effects of season or area. If we had included more large samples in our simulation, the linear relationship may not have been evident.

Calculation of *K* Values

Because all terms used to calculate Var ($\hat{N}$) equal $O(1/n)$ and Var ($\hat{N}$) is a linear sum of the terms, Var ($\hat{N}$) = $O(1/n)$ or CV ($\hat{N}$) = $O(1/\sqrt{n})$. Therefore, the relationship

$$\text{CV}(\hat{N}) = K/\sqrt{n} \tag{8}$$

can be used to determine the change in CV ($\hat{N}$) for various values of n, where K is a constant. This relationship is true if the number of schools sighted is proportional to population size. This seems to be a reasonable assumption, although a more complicated relationship between density and school size, based on dolphin social structure and its interaction with the fishery process, is possible. K values for spotted dolphins in the north and total areas were calculated for methods A and B using the 1977–83 data (Table 1). These K values were then used to determine CV ($\hat{N}$)s for specified values of n which would be expected assuming from one to three annual ship surveys.

Detection Rates

The number of expected sightings with use of one to three ships was calculated by computing detection rates as the average number of dolphin sightings per searching day. A day's searching effort generally consisted of searching from sunrise to sundown; therefore, we assumed most survey days covered approximately the same trackline distance. However, distance searched may vary inversely with rates of detecting dolphin schools because effort is halted so that observers can identify schools and make school size estimates. The number of survey days, and hence number of ships, required to obtain a specified CV ($\hat{N}$) was determined by dividing the number of required sightings by the rate of detecting schools.

Detection rates were caculated separately for data from the *Jordan* cruise and from the *Cromwell* cruise because of the wide disparity in detection rates of dolphins from the two vessels when operating simultaneously in the calibration area (Table 2). The *Jordan* has a much better platform from which to detect dolphins because its observation station was higher relative to the water and because the *Jordan* rode much smoother than the *Cromwell*. Pooled *Jordan* and *Cromwell* detection rates were calculated by standardizing the *Cromwell* rates to *Jordan* rates (Table 2) as

$$DR = \frac{R_j T_j + R_c T_c C}{T_j + T_c} \tag{9}$$

where DR = pooled standardized detection rate for all dolphin schools,
R_j = dolphin schools detected per day by observers aboard the *Jordan*,
R_c = dolphin schools detected per day by observers aboard the *Cromwell*,
T_j = days searched aboard the *Jordan*,

TABLE 2.—Detection rates of all dolphin schools from the *Jordan* and *Cromwell* in the calibration area and pooled standardized detection rates for both vessels combined calculated in each stratum. Standardized detection rates were calculated using the ratio of *Jordan* to *Cromwell* detection rates in the calibration area.

	Jordan (*J*)			*Cromwell* (*C*)			
Stratum/area	Number of schools (*n*)	Days searched (*D*)	*n*/*D*	Number of schools (*n*)	Days searched (*D*)	*n*/*D*	*J*/*C* ratio of detection rates
Calibration area	102	28	3.643	49	31	1.581	2.304
							Pooled standardized *n*/*D*
1. Inside	237	106	2.24	87	56	1.55	2.70
2. Middle	108	80	1.35	18	22	0.82	1.47
3. West	43	54	0.80	14	56	0.25	0.69
4. South	91	60	1.52	4	5	0.80	1.54
North area (Pooled strata 1-3)	388	226	1.72	119	128	0.93	1.87
Total area (Pooled strata 1-4)	479	282	1.70	123	132	0.93	1.84

T_c = days searched aboard the *Cromwell*, and

C = ratio of schools detected per day by observers aboard the *Jordan* in the calibration area during 1979 to schools detected per day by observers aboard the *Cromwell* in the calibration area during 1979.

The percent of searching days when one to three ships were used was allocated to each stratum (Table 3) by the square root of school density. The number of schools which would be expected to be detected based on the standardized detection rates then was calculated (Table 4).

TABLE 3.—Percent of searching days allocated by square root of density to each stratum in the north and total areas.

Stratum	North area	Total area
Inside	45.6	35.8
Middle	36.5	28.7
West	17.9	14.0
South	—	21.5

TABLE 4.—Number of days searched and number of schools detected per year of effort with use of 1, 2, or 3 ships allocated to the various strata by square root of density.

	North		Total	
Stratum	Number days	Number schools	Number days	Number schools
1 ship = 120 days				
Inside	55	149	43	116
Middle	44	65	34	50
West	21	14	17	12
South	—	—	26	40
Total	120	228	120	218
2 ships = 240 days				
Inside	110	298	86	232
Middle	88	130	68	100
West	42	28	34	24
South	—	—	52	80
Total	240	456	240	436
3 ships = 360 days				
Inside	165	447	129	348
Middle	132	195	102	150
West	63	42	51	36
South	—	—	78	120
Total	360	684	360	654

RESULTS

For either the north or total area, the same decrease in spotted dolphin populations can be detected 2 to 4 years earlier using method B, which uses pooled density and school size estimates, than when using method A, which uses estimates calculated for each stratum (Table 5). This is because large variances associated with the method A population size estimates occur due to small sample sizes in some strata. Therefore, method B was used in subsequent calculations.

The same number of years is required to detect a specific trend if the north or total areas are surveyed (Table 5). This result is true only if the 1977–83 data, which contain small sample sizes in the south stratum, are representative of future data. However, the northern offshore spotted dolphin stock occurs only in the north area and elimination of the south stratum will ensure better coverage of this north area, especially in the west stratum where sample sizes are minimal for applying the Fourier series model (Table 4). Therefore, subsequent calculations were made only for the north area. Annual population estimates for the northern stock would be biased only if substantial variation in the amount of dolphin migration between the north area and south stratum occurred during survey years.

TABLE 5.— Number of years required to detect an annual 5% decrease in spotted dolphin population size using 1, 2, or 3 ships and 2 different methods of pooling data. Method A utilized Equation (2) in text while method B utilized Equation (3). Alpha and beta levels equal 0.05, and effort was allocated to the various strata by square root of density. Number of schools expected to be detected each year determined using detection rates from Equation (9). K determined using Equation (8). CV ($\hat{N}$) denotes coefficient of variation of population abundance estimate.

Stratum	Number ships	Number schools	K	CV ($\hat{N}$)	Years required
North area					
Method A	1	228	4.05	0.27	17
	2	456		0.19	12
	3	684		0.15	11
Method B	1	228	3.06	0.20	13
	2	456		0.14	10
	3	684		0.12	9
Total area					
Method A	1	218	3.93	0.27	17
	2	436		0.19	12
	3	654		0.15	11
Method B	1	218	2.94	0.20	13
	2	436		0.14	10
	3	654		0.11	8

At the 5% error level, only rates of change of 11% per year or greater can be detected in a 5-yr survey period, even using three ships per year (Table 6). This is a rather high rate of decrease,

TABLE 6.—Minimum rates of annual decrease and minimum total decreases in spotted dolphin population size which could be detected in 5 years under different conditions. Changes were calculated for several alpha and beta levels, with a one-tailed test, using 1, 2, and 3 ships, for CV (*N*) determined using jackknife formulae, and data in the north area pooled over all strata (method B).

Number ships	CV (*N*)	Decrease per year	Total decrease
$\alpha = \beta = 0.05$			
1	0.20	0.19	0.65
2	0.14	0.13	0.50
3	0.12	0.11	0.44
$\alpha = \beta = 0.10$			
1	0.20	0.14	0.53
2	0.14	0.10	0.41
3	0.12	0.08	0.34
$\alpha = \beta = 0.20$			
1	0.20	0.09	0.38
2	0.14	0.06	0.27
3	0.12	0.05	0.23

and would lead to a 44% reduction in population size over the 5-yr period. If two or one ship is used, however, the minimum detectable rates of decrease are higher still, 13% and 19%, respectively. When the power of the survey design is considered, the same dilemma is evident (Table 7). Even when three ships are used, the power is acceptably high only if the rate of decrease is at least 10% per year. The probability of detecting a 5% per annum decrease at a 5% alpha level, for example, is only 0.51. This means that with a probability of 0.49 we would conclude that no decrease had taken place, when in fact it had. Power is even less if only one or two ships are used.

Alternatively, we may have either to conduct the surveys for more than 5 years and/or relax the acceptable alpha and beta error level (Table 8). With three ships and 5% error levels, 5 years is sufficient to detect a 10% per annum decline, but 9 years are required to detect a 5% per annum decline and 13 years are required to detect a 3% per annum decline. For alpha and beta levels equal 0.10 or 0.20 and use of three ships, a 5% decrease can be detected in 7 or 5 years, respectively.

TABLE 7.—Power, or the probability of detecting a decrease in spotted dolphin population size during a 5-yr period. Power was calculated for surveys using 1, 2, or 3 ships, for various rates of annual and total population decrease, and for testing the regression of population size against time at various significance levels (α).

Number of ships	CV (*N*)	Rate of decrease per year	Total decrease	Power when α = 0.05	0.10	0.20
1	0.20	0.01	0.05	0.08	0.14	0.26
		0.03	0.14	0.15	0.25	0.41
		0.05	0.23	0.26	0.40	0.57
		0.10	0.41	0.62	0.75	0.86
2	0.14	0.01	0.05	0.09	0.16	0.29
		0.03	0.14	0.22	0.34	0.52
		0.05	0.23	0.42	0.56	0.73
		0.10	0.41	0.87	0.93	0.97
3	0.12	0.01	0.05	0.10	0.18	0.31
		0.03	0.14	0.27	0.40	0.57
		0.05	0.23	0.51	0.66	0.80
		0.10	0.41	0.94	0.97	0.99

TABLE 8.—Number of years required to detect various annual decreases and total declines of spotted dolphins calculated for several alpha and beta levels using 1, 2, and 3 ships. CV (*N*)s were calculated using jackknife formulae and using data in the north area pooled over all strata (method B).

Number ships	CV (*N*)	Decrease per year	Number years required	Total decrease
$\alpha = \beta = 0.05$				
1	0.20	0.01	39	0.32
		0.03	19	0.44
		0.05	13	0.49
		0.10	8	0.57
2	0.14	0.01	30	0.26
		0.03	14	0.35
		0.05	10	0.40
		0.10	6	0.47
3	0.12	0.01	27	0.24
		0.03	13	0.33
		0.05	9	0.37
		0.10	5	0.41
$\alpha = \beta = 0.10$				
1	0.20	0.01	32	0.28
		0.03	15	0.37
		0.05	11	0.43
		0.10	7	0.52
2	0.14	0.01	25	0.22
		0.03	12	0.31
		0.05	8	0.34
		0.10	5	0.41
3	0.12	0.01	23	0.21
		0.03	11	0.29
		0.05	7	0.30
		0.10	5	0.41
$\alpha = \beta = 0.20$				
1	0.20	0.01	24	0.21
		0.03	11	0.29
		0.05	8	0.34
		0.10	4	0.34
2	0.14	0.01	19	0.17
		0.03	8	0.22
		0.05	6	0.26
		0.10	3	0.27
3	0.12	0.01	17	0.16
		0.03	8	0.22
		0.05	5	0.23
		0.10	3	0.27

DISCUSSION

Our analyses indicate that our ability to detect changes in the size of spotted dolphin populations in the eastern tropical Pacific is not very great without substantial long-term ship time. This is not surprising given the vast area of ocean inhabited by the dolphins and the low sighting rate from ships. We feel our results represent a generally accurate picture based on available data. However, the analyses must be qualified by noting that the data used to generate these results were accumulated during all seasons over 5 years. Data collected in the future will come from surveys conducted at the same time each year and may be less variable. In addition, more precise data gathering techniques or data fitting models may become available. If so, these factors would yield greater ability to detect lower rates of decrease, greater power, and lower required number of years. On the other hand, the estimates of expected variance have dealt with survey precision (measurement error) only. If environmental variability is important, data collected in future surveys may be more variable than we have calculated. In long-lived animals with many year classes contributing to reproduction, however, environmental variability will tend to be less important than survey imprecision (Gerrodette in press).

The selection of appropriate alpha and beta errors levels depends on one's perspective. An alpha error would occur if we concluded that a decrease in dolphin abundance was occurring when in fact it was not. It is therefore of interest to the tuna industry to minimize this type of error. A beta error would occur if we concluded that no decrease in dolphin abundance was occurring when in fact it was. It is in the interest of conservation groups to minimize this type of error. As is well known in statistical theory, however, there is a trade off between the two types of error, a decrease in one leads to an increase in the other. In our analyses we have balanced the two types of error by making alpha and beta equal. We have also used a range of equal alpha and beta levels (0.05, 0.10, and 0.20) to illustrate how choice of error level can affect sampling design. Higher tolerance of error leads to lower rates of decrease which could be detected in shorter times, but, of course, one is less sure of the conclusions reached. Thus the choice of acceptable alpha and beta levels to use in detecting changes in spotted dolphin population size is a management decision based primarily on social rather than statistical criteria.

At least two ships are required to provide representative coverage of the survey area. Although use of a third ship provides better coverage, it does not substantially improve detection of population decreases. For alpha and beta levels of 0.05, a 5% per year decrease can be detected in 9 years with use of three ships or 10 years with use of two ships (Table 8). For other alpha and beta levels, use of the third ship only increases our ability to detect specific decreases by about 1 year. Given the annual cost of each ship, it would be more cost-effective to conduct the surveys for an additional year using only two ships. Another strategy is to conduct surveys less frequently than annually. Gerrodette (in press) provides a numerical example of this approach. For parameter values appropriate to spotted dolphins, conducting surveys less frequently than annually (every second or third year, for example) could save substantial ship time, but more years would elapse before a trend was detected.

If a 5% annual decrease in population size occurred, the number of spotted dolphins killed would have to be large. Assuming a spotted dolphin population of 2.5 million animals (Table 1) and disregarding natural mortality and reproduction, approximately 125,000 animals would be killed each year. The estimates of all dolphins taken by the fishery during each of the last few years are only about 40,000 animals per year (Hammond and Tsai 1983). It may be unreasonable to expect annual decreases at the 5% annual level; rather decreases of 3% or 1% per year would be more reasonable. If so, two ships would require at least 14 years to detect the decline (Table 8).

Nonetheless, the number of dolphins actually killed may exceed 40,000 animals per year because dolphin mortality aboard the unsampled trips of U.S. and non-U.S. registered vessels, which is assumed to be similar to that on the sampled trips, may in fact be substantially higher. In addition, the effects of chasing and capturing dolphins several times per year are not estimated in our analyses.

Techniques and data are presented in our paper to determine the optimal number of ships and number of years required to detect decreases in spotted dolphin populations in the eastern tropical Pacific. However, these techniques are applicable to investigate the amount of effort and time required to monitor changes in any appropriate population index for any species where sufficient

data exists or can be collected to determine reasonable estimates of coefficient of variation.

SUMMARY

Use of three ships provides excellent physical coverage of the eastern tropical Pacific dolphin area. Coverage using two ships appears adequate while use of one ship yields very sparse coverage.

Assuming alpha and beta levels of 0.05, use of two ships for each of 5 years will only allow us to detect a 13% annual decrease in spotted dolphin abundance. This means that the population could decline by 50% during the survey period before it could be detected. If three ships are used for 9 years, a 5% decrease per year could be detected.

Use of two ships instead of three only decreases our ability to detect specific trends by about 1 year. For alpha and beta levels of 0.05, use of two ships will allow detection of a 5% annual decrease in 10 years, instead of 9 with three ships.

The sampling period may be shortened if larger alpha and beta levels and larger annual decreases are acceptable. For alpha and beta levels of 0.10, use of two ships will allow detection of a 10% annual decrease after 5 years during which a 41% decrease in the population could occur.

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A TRAWL SURVEY METHOD FOR ESTIMATING LOGGERHEAD TURTLE, *CARETTA CARETTA*, ABUNDANCE IN FIVE EASTERN FLORIDA CHANNELS AND INLETS

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ABSTRACT

Five eastern Florida navigational channels were surveyed on a quarterly basis from November 1981 through August 1982. The purpose of the surveys was to provide estimates of loggerhead turtle abundance for each channel over all seasons of the year. Standard methods for estimating loggerhead turtle abundance from trawl samples were developed, and the probability of capture in a 30 m by 1,483 m substation ($\bar{P}$) was estimated to be 0.28 ± 0.05 (95% confidence level). Abundance estimates based on this probability of capture were then developed for each channel and survey. Of the channels surveyed, only Port Canaveral harbored significant concentrations of loggerhead turtles; populations ranged from 701 ± 291 turtles in February to a low of 38 ± 26 turtles in August. A few loggerhead turtles were captured in the other channels, but infrequency of occurrence suggested random encounters rather than areas of concentration.

In the western Atlantic Ocean, loggerhead turtles, *Caretta caretta*, forage throughout the warm waters of the continental shelf from Argentina northward to Nova Scotia, including the Gulf of Mexico and the Caribbean Sea (Carr 1952). On a seasonal basis, loggerheads are common as far north as the Canadian portions of the Gulf of Maine (Lazell 1980), but during cooler months of the year distributions shift to the south (Shoop et al. 1981). Sporadic nesting occurs throughout the tropical and warm temperate range of distribution, but the most important nesting areas are the Atlantic coast of Florida, Georgia, and South Carolina (Carr and Carr 1978). The Florida nesting population of *Caretta* has been estimated to be the second largest in the world (Ross 1982).

Although population levels of adult female loggerheads can be estimated from counts on nesting beaches, the remaining animals (males, subadults, and nonbreeding females) do not come ashore and are not readily available for census. To estimate the total number of loggerheads in an area, all segments of the population should be considered.

In the vicinity of Cape Canaveral, FL, loggerhead turtles congregate in the Port Canaveral ship channel (Carr et al. 1980). Because turtles can be captured and studied in this unique area throughout the year, the National Marine Fisheries Service (NMFS) has conducted surveys to monitor population levels and estimate relative turtle abundance. This study is a continuation and expansion of research efforts which began in 1978.

Presented are results of a 1-yr investigation conducted in response to requests from the U.S. Army Corps of Engineers (COE) and the U.S. Navy, to estimate sea turtle abundance and seasonality in five eastern Florida navigational channels. Animals captured in this study were subadults, adult males, and adult females. Population estimates of subadult turtles may prove to be particularly useful for management, as efficacy of conservation measures should be first evident in the population levels of the youngest cohorts.

Results of this study provide a reliable index of loggerhead turtle abundance for the study year and an alternative to population estimates based only on nesting females. Most importantly, for the first time, a standard method has been developed that provides sea turtle abundance estimates with approximate standard errors.

STUDY AREAS

Five eastern Florida navigational channels were surveyed on a seasonal basis over the study period. A description of the survey sites follows (each site is diagramed in Figure 1):

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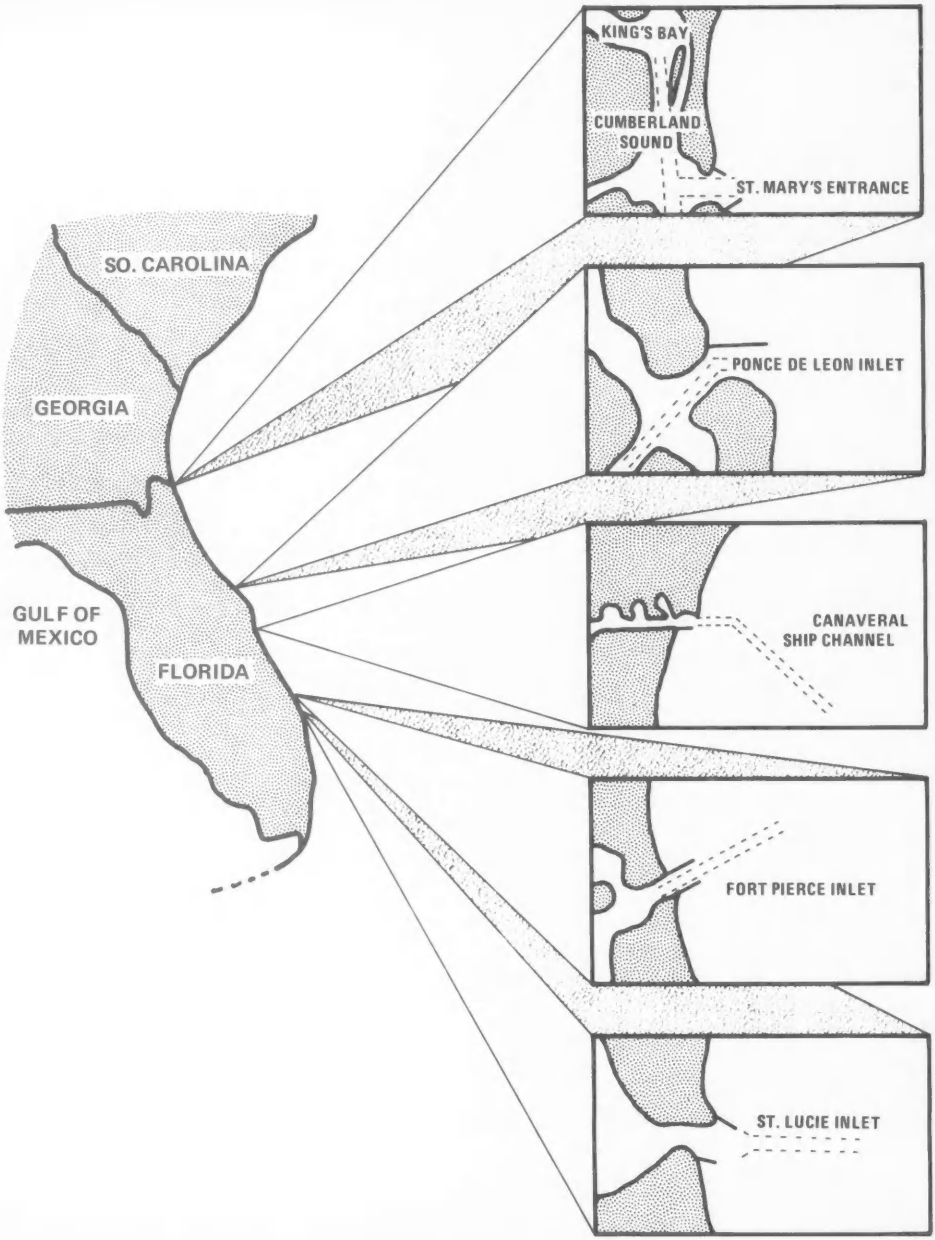

FIGURE 1.—Description of five eastern Florida navigational channels and inlets surveyed.

1) St. Mary's entrance to King's Bay (lat. 30°43′N, long. 80°20′W) is divided by the state boundary between Georgia and Florida and includes Cumberland Sound through which the Intracoastal Waterway connects King's Bay with the entrance channel. Mud predominates inside of the jetties, and mud and rock bottom are found in the channel offshore.

2) Ponce de Leon Inlet (lat. 29°04′N, long. 80°53′W), on the northeast coast of Florida, is a small inlet accessible only to small craft. A jetty protects the inlet to the north; inside the inlet a narrow channel leads to the Intracoastal Waterway. The substrate is hard sand and silt with scattered rubble.

3) The Port Canaveral ship channel is located on the central east coast of Florida (lat. 28°23′N, long. 80°33′W). The ship channel allows navigation from offshore, through a manmade inlet, into a protected harbor. A depth of 11 to 13 m is maintained by dredging. Soft mud and detritus bottom is found in the channel and sand-clay in the surrounding areas.

4) Fort Pierce Inlet (lat. 27°28′N, long. 80°16′W) is located on the south-central east coast of Florida. The channel allows navigation from offshore, through the inlet that is protected by jetties, into the Intracoastal Waterway. The bottom is hard sand and rubble.

5) St. Lucie Inlet, also on the south-central east coast of Florida (lat. 27°09′N, long. 80°07′W), is another small inlet with use limited to small craft. A completed jetty protects the north side of the inlet and a second jetty was under construction to the south during the survey periods. The substrate offshore is sloping hard sand and silt.

MATERIALS AND METHODS

Quarterly trawl surveys of the navigational channels were conducted from November 1981 through August 1982. During each survey, the Port Canaveral ship channel was sampled twice and the remaining four sites (St. Mary's entrance, Ponce de Leon Inlet, Fort Pierce Inlet, and St. Lucie Inlet) were sampled once. A standard 18 m "mongoose" fish trawl, spread by 3 m × 1 m trawl doors and equipped with mudrollers, was used throughout the study period.

Prior to the surveys, the boundaries of each channel were located using National Ocean Surveys charts and subdivided by a grid pattern for systematic sampling. Lengthwise, each channel was separated into 1,483 m stations which were divided into 30 m wide substations (Fig. 2). The number of substations in each station was dependent on channel width.

A systematic sampling scheme was devised to sample each channel substation: every other station was sampled in leapfrog fashion in one direction, and then the direction was reversed. The substation sampled within each station was determined by random drawing without replacement and sampling continued until all substations were occupied. This approach avoided the "edge effect", but allowed samples to be statistically treated as random (Milne 1959). Control stations outside the channel were sampled at all sites during each survey period.

In addition to standard survey procedures, experiments designed to estimate gear efficiency were conducted in the Port Canaveral ship channel. Following each survey, a substation with abundant loggerhead turtles was selected and a series of repetitive tows performed. All loggerheads captured during these experiments were tagged and released on station prior to the next tow. As this was essentially a "removal" method, any recaptures of loggerhead turtles tagged during the experiment were not considered as part of the catch and were excluded from analysis. Tows were continued in rapid order until two consecutive samples yielded zero catches or the working day ended.

ANALYTICAL PROCEDURES

The efficiency of the sampling gear was established before population estimates were computed. The probability of loggerhead turtle capture ($\hat{P}$) was estimated for each repetitive towing experiment using the formula:

$$\hat{P} = C_1/\hat{N}_0$$

where C_1 = catch on the first tow in the substation

$\hat{N}_0$ = estimated number of loggerhead turtles in the substation.

A regression of cumulative loggerhead turtle catch (Y) on catch per sample (X), expressed as $Y = b_0 + b_1X$, was used to estimate (N_0) based on the relationship: $\hat{N}_0 = b_0$. The estimated variance of N_0 was calculated according to procedures of Kleinbaum and Kupper (1978):

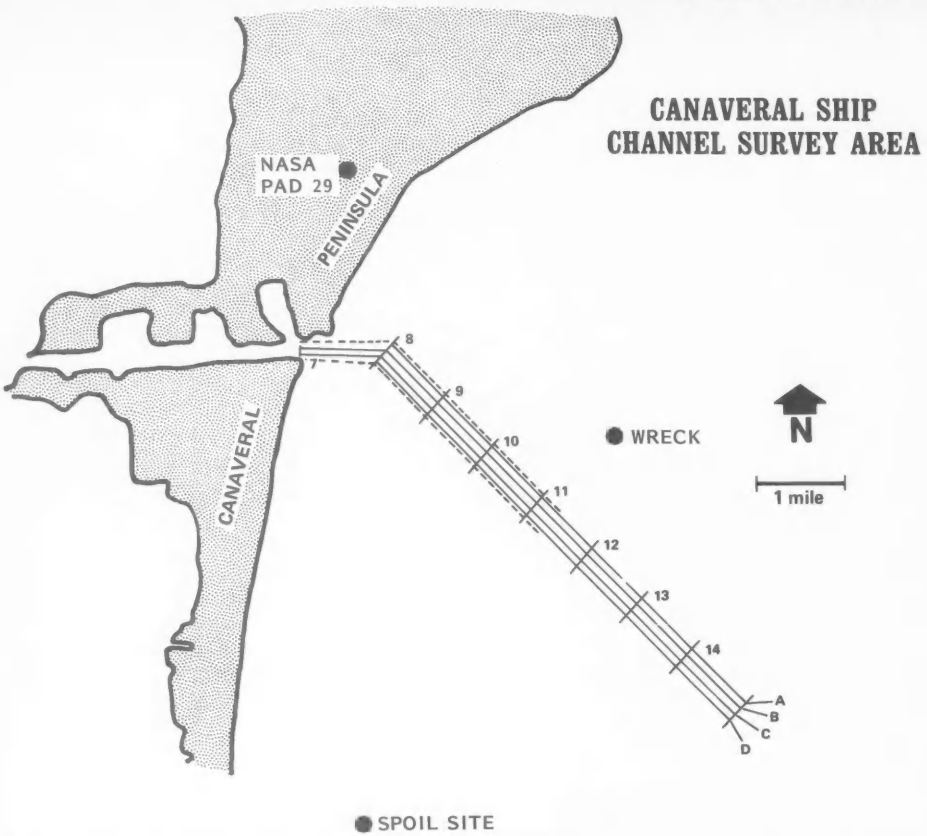

FIGURE 2.—Description of the Port Canaveral ship channel survey area. The channel was separated into 1,483 m stations (7-14), which were divided into 30 m wide substations (A, B, C, and D).

$$\text{Var}\,(\hat{N}_0) = (\text{SE})^2\,[1/n + \overline{X}^2/\Sigma(X_i - \overline{X})^2]$$

where SE = standard error of the estimate provided by the straight line fit
n = sample size of the catch data set
X_i = observed catch per sample in the i^{th} sample and

$$\Sigma(X_i - \overline{X})^2 = \Sigma X_i^2 - \Sigma(X_i)^2/n.$$

The estimated variance of P was then calculated using procedures of Mood et al. (1974):

$$\text{Var}\,(\hat{P}) = (C_1/\hat{N}_0^2)^2\,\text{Var}\,\hat{N}_0.$$

In one instance, the experiment was conducted in an area larger than the standard substation and a ratio (standard area/larger area = 0.75) was used as a constant multiplier to standardize estimates.

The mean probability of capture was calculated by combining all experimental P's using the formulae:

$$\hat{\bar{P}} = \hat{P}_i/k, \text{ and Var}\,(\hat{\bar{P}}) = \text{Var}\,(\hat{P}_i)/k^2$$

where k = number of estimates.

Once the efficiency of trawling equipment had been determined, the number of loggerhead turtles present in a substation ($\hat{N}$) was estimated using the following formula (Seber 1973):

$$\hat{N} = C/\hat{P}$$

where $\hat{P}$ = probability of capture
C = number of animals captured.

If more than one sample tow was made in a substation, the mean catch ($\overline{C}$) was substituted in the above formula. To estimate the number of loggerhead turtles in a channel substation, station, or the entire channel, the mean number captured per substation sample ($\overline{C}$) times the number of substations (s) was substituted: $\hat{N} = s\overline{C}/\hat{\overline{P}}$. The estimated variance of this estimate is (Mood et al. 1974):

$$\text{Var}(\hat{N}) = (s/\hat{\overline{P}})^2 [\text{Var}(\overline{C}) + (\overline{C}/\hat{\overline{P}})^2 \text{Var}(\hat{\overline{P}})] .$$

RESULTS

Estimates of the probability of capture and associated standard error estimates from nine repetitive trawl experiments are presented in Table 1. Estimated probability of capture within a substation based on six experiments ranged from 0.21 to 0.31 ($\hat{\overline{P}} = 0.28$; 95% confidence interval = ±0.05; estimated variance = 5.18×10^{-4}). Three experiments were excluded from the analyses: two were discarded because the catch failed to decline due to low population levels, and a third was eliminated because of problems with the sampling trawl.

Estimates of loggerhead turtle abundance by survey for the Port Canaveral ship channel ranged from 701 ± 291 turtles in late February 1982 to a low value of 38 ± 26 turtles in late August 1982 (Table 2). Port Canaveral channel stations 9 through 11 (Fig. 2) exhibited the highest loggerhead turtle abundance during all seasons of the year. Mean catch for all samples in the channel was 2.55 turtles/tow and 0.50 turtles/tow for control samples, supporting the hypothesis that loggerhead turtles congregate in the Port Canaveral ship channel.

Loggerhead turtle abundance estimates for the remaining four survey sites were low during all seasons of the year (Table 3). Over the study period, a total of 18 loggerhead turtles was captured: 2 at St. Mary's entrance, 6 at Ponce de Leon Inlet, 3 at Fort Pierce Inlet, and 7 at St. Lucie Inlet.

DISCUSSION

Our estimates of the probability of capture were based on the supposition that catch-per-tow in a given substation will decrease as loggerhead turtles are removed. The regression of cumulative loggerhead turtle catch on catch per sample can then be used to estimate the orginal population size in the substation (Brownlee 1965) and using this estimate, the probability of capture can be computed. Assumptions associated with this procedure are a closed population, the trawl fishes only within the defined bounds of the substation, each tow is an equal unit of effort and the probability of capture remains constant.

TABLE 1.—Estimated probability of loggerhead turtle capture in a Port Canaveral ship channel substation using an 18 m fish trawl.

Date	Catch on first tow (C_1)	Population estimate ($\hat{N}_0$)	Probability of capture ($\hat{P}$)	SE ($\hat{P}$)	Approximate 95% C.I. (P)
11/6/81	8	20.19	0.40	0.09	±0.17
12/5/81	6	19.54	0.31	0.01	±0.02
12/7/81	13	51.48	0.28	0.03	±0.07
2/28/82	7	30.31	0.23	0.02	±0.04
3/2/82	15	72.85	0.21	0.07	±0.13
5/23/82	2	(*)			
5/28/82	2	(*)			
6/1/82	1	(*)			
8/6/82	3	11.82	0.25	0.05	±0.10
mean ($\hat{P}$)			0.28	0.03	±0.05

[1]Data set discarded.

TABLE 2.—Estimated number of loggerhead turtles ($\hat{N}$) at Port Canaveral ship channel by station and survey period (1981-1982).

Station	Nov. 3-5	Dec. 2-4	Feb. 3-6	Feb. 21-26	May 7-12	May 28-June 1	Aug. 4-5	Aug. 20-22
7	[1]	[1]	[2]0	[2]0	[2]21	[2]0	[2]14	[2]0
8	[1]	[1]	25	43	29	11	21	0
9	93	32	114	143	[2]29	21	57	7
10	64	32	254	221	32	21	61	18
11	21	7	[3]157	146	21	36	8	7
12	21	4	43	89	7	21	4	4
13	0	0	0	11	[2]10	0	0	0
14	0	0	0	4	[2]0	[2]0	0	0
Chanel	[4]200	[4]75	632	701	152	122	168	38
Approx. 95% C.I.	±129	±50	±314	±291	±86	±62	±82	±26

[1]Station not sampled.
[2]Station incompletely sampled.
[3]Includes 4 Kemp's ridley turtles, *Lepidochelys kempi*.
[4]Estimate is for stations 9-14, others are for 7-14.

TABLE 3.—Estimated loggerhead turtle abundance during quarterly surveys of St. Mary's entrance—King's Bay, Ponce de Leon Inlet, Ft. Pierce Inlet and St. Lucie Inlet.

Date	St. Mary's King's Bay	Ponce de Leon Inlet	Fort Pierce Inlet	St. Lucie Inlet
11/81	9 ± 18	0	0	0
2/82	0	11 ± 15	4 ± 7	4 ± 7
5/82	0	0	4 ± 8	11 ± 11
8/82	0	0	0	4 ± 7

Although these assumptions may not be satisfied in all cases, our estimates of probability of capture in a given substation were consistent except for the two discarded experiments conducted during periods of low loggerhead turtle densities. These findings suggest that some loggerheads encountering the trawl were able to avoid capture, presumably by moving out of the trawl path. The results also indicate that a consistent percentage of loggerheads were captured by the trawl, facilitating the estimation of turtle abundance based on number of turtles captured. It should be noted that the probability of capture in a given substation (as presented in our results) is lower than the probability of capture in a given tow. To compute the probability of capture in a single tow, the width of the substation is divided by the width of the trawl and this factor multiplied by the probability of capture in the substation.

Loggerhead turtle abundance estimates in the Port Canaveral ship channel exhibited large seasonal variation (Table 2). The estimated population levels during the month of February were significantly higher than all other quarterly surveys indicating that loggerheads were most abundant during winter months. These findings are in agreement with other NMFS surveys in the Canaveral channel from 1978 to 1983 (Table 4) and support the contention of Carr et al. (1980) that loggerhead turtles may hibernate in the Port Canaveral channel in refuge from low water temperatures. The fact that the winter of 1981-82 was unusually mild, could account for the lack of an early winter peak in loggerhead turtle abundance observed in previous years.

Data presented in Table 4, while of limited statistical value due to inconsistencies in sampling methodologies, are useful for comparisons between this study and other NMFS Canaveral channel surveys. It is worthy of note that mean catch per unit effort (CPUE) by month combining all years was in excess of 10 loggerhead turtles/hour from November through March with peak concentrations in February and March. Lowest CPUE values and presumably population levels occurred from April through September, which is in agreement with our findings.

It is evident that loggerhead turtle abundance estimates were highly variable between surveys made in the same quarter (Table 2). We speculate that these fluctuations in population levels were caused by short-term immigration and emigration in response to local weather changes. We have observed daily changes in catch rates which appear to be correlated with passage of weather fronts.

Distribution of loggerhead turtles within the Port Canaveral ship channel is also of interest. In every survey, stations 9, 10, and 11 exhibited the highest abundances, suggesting that they were preferred turtle habitat. Stations 7, 8, and 12 exhibited intermediate population levels and stations 13 and 14 had low turtle abundance levels. Stations 7, 8, 9, and 10 were those where deepest cuts into the seabed have been made by dredging. The bottom was characterized by divers as clay-silt and detritus as opposed to the harder clay-sand bottom outside the channel (Carr et al. 1980).

Interpretation of loggerhead turtle abundance estimates generated from this study is complicated by the fact that three different groups of

TABLE 4.—Summary of catch per unit effort (CPUE) of loggerhead turtles in the Port Canaveral ship channel (1978-83). Values are in turtles per hour standardized to a single 100-ft net. N = number of tows.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1978		37.74 $N = 7$	55.73 $N = 7$							18.99 $N = 5$	10.82 $N = 10$	21.64 $N = 14$
1979	11.56 $N = 17$	11.88 $N = 11$	8.21 $N = 11$	9.13 $N = 3$	1.33 $N = 5$	21.25 $N = 16$	13.86 $N = 32$		9.43 $N = 28$			
1980	24.82 $N = 19$	19.61 $N = 40$	28.57 $N = 77$		3.38 $N = 22$	3.77 $N = 22$	3.31 $N = 60$	3.29 $N = 152$	2.62 $N = 189$	5.44 $N = 135$	11.81 $N = 105$	5.11 $N = 7$
1981		15.89 $N = 12$		11.22 $N = 16$				7.88 $N = 41$	3.26 $N = 51$		22.06 $N = 29$	7.18 $N = 42$
1982		41.83 $N = 99$	58.53 $N = 14$		7.49 $N = 96$	4.24 $N = 15$		5.95 $N = 83$				
1983			4.86 $N = 20$	2.35 $N = 60$								
Totals	18.56 $N = 36$	32.61 $N = 169$	27.88 $N = 129$	4.21 $N = 79$	6.50 $N = 123$	9.18 $N = 53$	6.98 $N = 92$	4.77 $N = 276$	3.45 $N = 268$	5.92 $N = 140$	13.80 $N = 144$	10.16 $N = 63$

loggerheads (adult males, adult females, and subadults) utilize the channel at different times of the year (Henwood 1987). Adult males are dominant in April and May, adult females are most abundant from May through August and subadult turtles are predominant during the remainder of the year. For this reason, direct comparisons between quarterly surveys may be inappropriate.

It is unfortunate that the three discarded repetitive trawl experiments occurred in May and June when the population was comprised primarily of breeding adults. Low population levels at this time may reflect a reduced catchability coefficient in adult loggerhead turtles possibly associated with behavioral changes. The ability of loggerhead turtles to escape trawls may also be enhanced during periods of high water temperatures, but no evidence of this was noted during August or November.

Loggerhead turtle abundance in the remaining four channels was low during all quarterly surveys. These findings confirm the presence of loggerhead turtles along much of Florida's eastern coastline, but do not indicate any channel areas with turtle concentrations similar to Port Canaveral. It is of special interest that only Port Canaveral, a manmade habitat, harbors concentrations of loggerhead turtles throughout the year and particularly during winter months.

The St. Mary's entrance to King's Bay survey area was by far the largest site investigated and may have been incompletely sampled relative to the total area involved. This location was of particular interest to the U.S. Navy because of planned construction of a Trident submarine base in King's Bay. Although no concentrations of loggerhead turtles were noted over the course of this investigation, future dredging of this channel could potentially result in a situation similar to Port Canaveral, with loggerhead turtles congregating in a deepwater manmade habitat.

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HOMING MIGRATION OF SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, TO THE FRASER RIVER

C. GROOT[1] AND T. P. QUINN[2]

ABSTRACT

Adult sockeye salmon, *Oncorhynchus nerka*, return to the Fraser River via either of two routes: a northern route through Queen Charlotte Strait, Johnstone Strait, and the Strait of Georgia between the mainland and Vancouver Island, and a southern route along the west coast of Vancouver Island and through Juan de Fuca Strait. The proportions of the total run of sockeye salmon using the two routes varies substantially from year to year. Understanding the factors influencing the migratory routes of Fraser River sockeye salmon provides a basis for forecasting the coastal migrations of salmon as they make the transition between oceanic and riverine environments. Our analysis of west coast troll catch and high seas tag-recovery data indicates that the salmon make landfall in different coastal regions from year to year. If the majority of Fraser sockeye approach the coast of Vancouver Island, then most will migrate via the Strait of Juan de Fuca. However, when landfall occurs north of Vancouver Island in the Queen Charlotte Sound area, most homeward migrating Fraser sockeye will travel through Johnstone Strait. Northern diversion rates of Fraser River sockeye salmon for the period 1953-77 were positively correlated with Fraser River discharge. For the period 1978-85 a strong positive correlation was evident with sea surface temperature (SST) along the northwest coast of Vancouver Island (Kains Island lighthouse). We conclude that Fraser River discharge and SST in the vicinity of Kains Island do not guide sockeye salmon in any direct way during their coastal approach, but that they reflect oceanographic conditions that affect salmon migrations directly or indirectly by acting on the feeding distribution, distance, or direction they must travel to reach home.

The Fraser River in British Columbia, Canada, is among the most important producers of sockeye salmon, *Oncorhynchus nerka*, in North America. Forty to sixty separate stocks, inhabiting the different lakes of its watershed, produce 2 to 20 million adults yearly (IPSFC 1954-1985). Sockeye salmon from the Fraser River system generally spend 1 year in nursery lakes after emergence and then migrate to sea as smolts. Most spend two winters in the ocean, returning to spawn in their home river as 4-yr-olds. To reach the Fraser River from their ocean feeding grounds they can take either of two routes around Vancouver Island (Fig. 1). From 1953 until 1977, the majority homed via the southern route through the Strait of Juan de Fuca (average 84%, range 65-98%). Since 1978, a larger proportion of sockeye have migrated via the northern route through Johnstone Strait (average through Juan de Fuca Strait 56%, range 20-78%) (IPSFC 1954-1986).

In 1958 a relatively high proportion (35%) of Fraser River sockeye salmon returned via the northern route. A large number of fish did not make landfall off the west coast of Vancouver Island but rather arrived in the more northerly Queen Charlotte Sound area (Tully et al. 1960) (Fig. 1). This coincided with anomalously high water temperatures off the coast of British Columbia. Tully et al. (1960) and Royal and Tully (1961) suggested that intrusion of warm water from the south in 1958 directed the homing sockeye salmon northward and closer to the mainland. Moreover, the fish appeared 10 days later in the fishery around Vancouver Island and over a longer period than usual, suggesting that they might have detoured around the area of warm water and made their coastal approach in the cooler nearshore waters. Alternatively, they might have initiated their homeward migration later or from a more distant area than usual.

Favorite (1961), on the other hand, took the view that the unusual extent of dilute seawater of Fraser River origin offshore from Queen Charlotte Sound in 1958 determined the location where the migrating sockeye entered coastal water. He assumed that homeward migrating salmon are attracted to dilute seawater contain-

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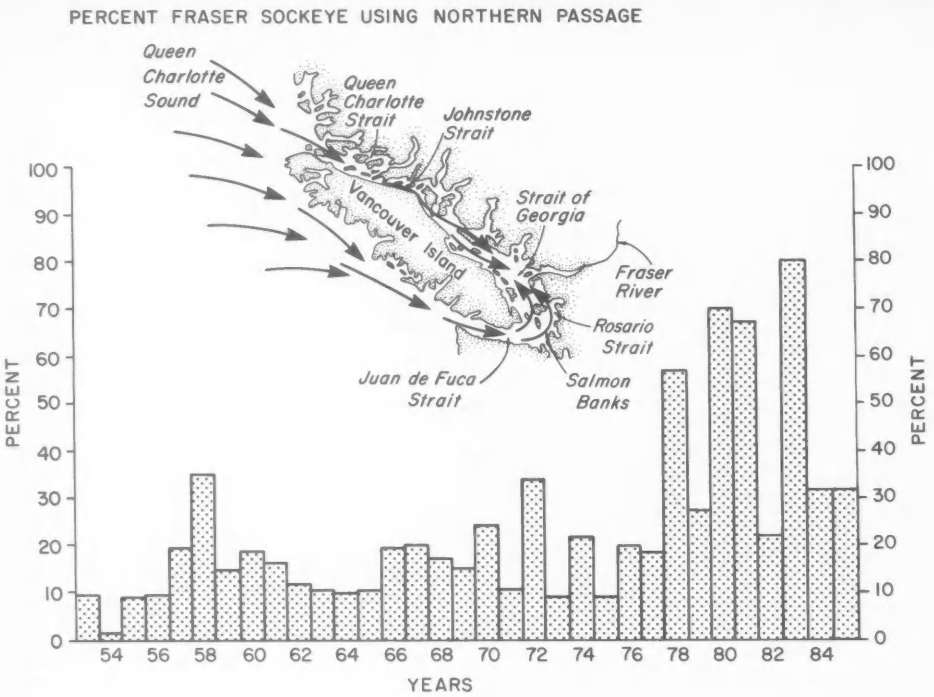


FIGURE 1.—Migratory routes of adult sockeye salmon returning to the Fraser River around Vancouver Island. The bar graph indicates the proportion of the total run that was estimated to have used the northern route (data from IPSFC annual reports).

ing homestream odors. Wickett (1977) extended this hypothesis by using indices of oceanographic processes to indicate the extent of dilute water plumes off Queen Charlotte Sound from 1953 to 1976. He concluded that the large proportion of Fraser River water discharged into the ocean northwest of Vancouver Island increased the rate of Fraser sockeye migrating through Johnstone Strait. The assumptions by Favorite (1961) and Wickett (1977) were influenced by the proposal of Hasler and Wisby (1951) that riverine odors learned during sensitive juvenile stages guide the homeward migration of adults in nearshore and river environments (Hasler 1966; Hasler and Scholz 1983).

We evaluated the extent to which oceanographic conditions in offshore waters influence the migratory routes of returning Fraser River sockeye around Vancouver Island. Nine more years of data (1977-85) have become available since Wickett's (1977) publication and four of these show unprecedented (57% to 80%) diversion rates via Johnstone Strait.

COASTAL MIGRATORY PATHWAYS OF FRASER RIVER SOCKEYE

INPFC Data

Under the auspices of the International North Pacific Fisheries Commission, Canada, the United States and Japan tagged 99,576 sockeye salmon in the North Pacific Ocean east of long. 165°E between 1956 and 1983. Of these, 4,842 were recovered, mostly (99.4%) along the coast of British Columbia and Alaska (INPFC 1984). We isolated data on Fraser River sockeye salmon from this larger data set to determine the migratory routes of these salmon. In the waters around Vancouver Island, 745 sockeye salmon were recovered. Since sockeye salmon home accurately (Ricker 1972; Foerster 1968; Quinn 1985), the

high seas tagging locations of the recovered fish give information on the distribution of Fraser River sockeye in the ocean. Southern British Columbia sockeye (of which at least 90% are Fraser River fish) were distributed in the Gulf of Alaska southward to lat. 45°N and westward to long. 178°E, a distance of 6,600 km from the Fraser River. The monthly changes in distribution of tagged fish from April to August and recovered in the year of tagging suggest that during spring and summer there is first a shift northeastward in May and June and then southeastward in July and August along southeast Alaska and the Queen Charlotte Islands towards Vancouver Island (Fig. 2). The findings are in accordance with the migration model for southeast British Columbia sockeye salmon presented by French et al. (1976).

Further indications of the coastal approach routes of Fraser River sockeye salmon can be derived from the rate of travel and the assumed direction of movement. From the positions and the dates of tagging and recovery, the rate of travel along the shortest route can be calculated for each fish. The rates ranged up to 98 km/day (4.1 km/hour or about 2 body lengths/second). Sonic tracking studies by Madison et al. (1972), Stasko et al. (1976), and Quinn and terHart (in press) showed that sockeye salmon travel at average speeds of 1.8 to 2.2 km/hour (about 1 body length/second) when migrating, which approximates the optimum sustained swimming speed for mature sockeye in endurance tests (Brett 1983).

For 373 sockeye salmon that were tagged 1,000 km or more away from the Fraser River and recovered around Vancouver Island, 86 (or 23%) travelled at speeds greater than 45 km/day (1.9 km/hour or about 1 body length/second) (Fig. 3). These estimates of swimming speed discount any effect of currents. Current direction and speed vary considerably in the regions through which

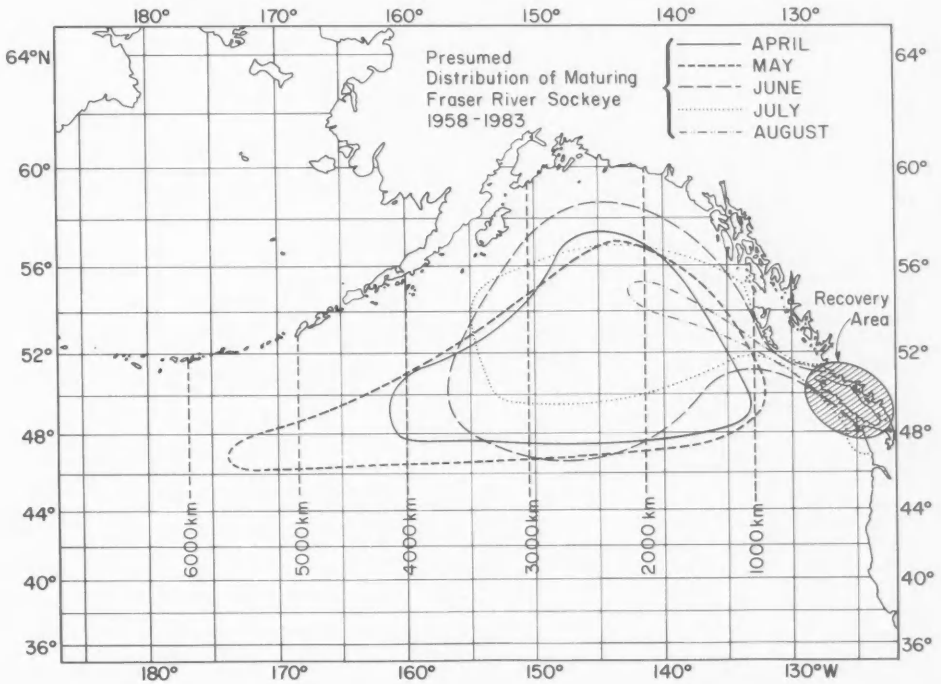


FIGURE 2.—Distributions in the Gulf of Alaska of releases of sockeye salmon from April through August that were recovered during the year of tagging around Vancouver Island, 1953-85.

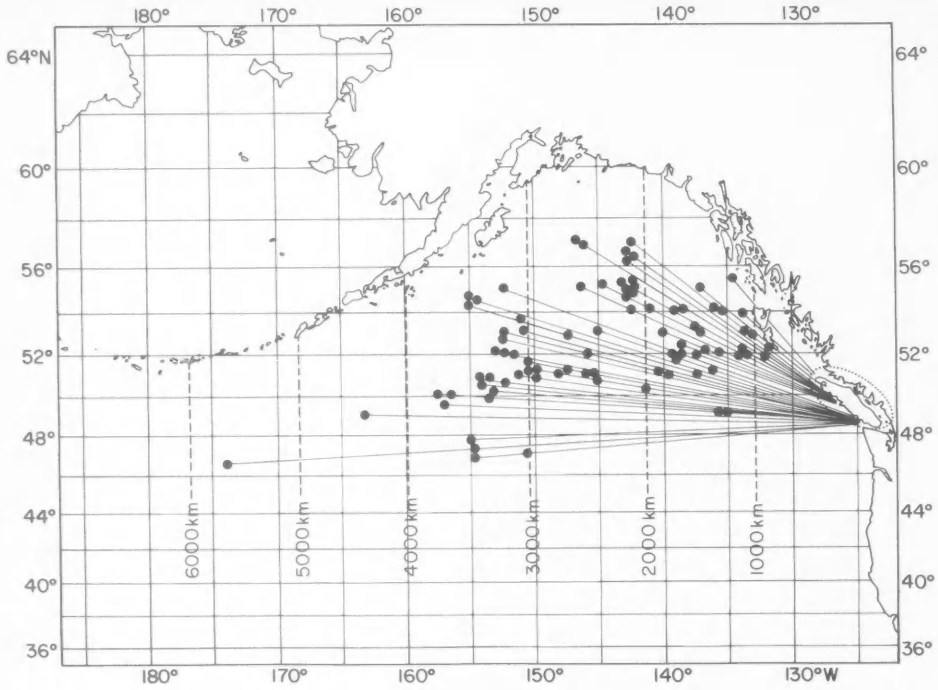


FIGURE 3.—Locations where maturing sockeye salmon were tagged and recovered in the Vancouver Island area. Only recoveries farther than 1,000 km away from the entrance of the Fraser River and with speeds over 45 km/day are illustrated.

the sockeye migrate but are usually less than 0.4 km/hour (Favorite et al. 1976; Tabata 1984). We assume that these fish must have travelled on relatively direct courses, day and night, based on the optimum speed of sockeye salmon (~2 km/hour) and the fact that substantial divergence from straight-line travel would have required the salmon to exceed their fatigue speed of 5 km/hour to accomplish the observed displacements (Quinn 1984; Quinn and Groot 1984). Connecting the tagging positions of these 86 sockeye salmon with the mouth of the home river shows that they must have approached Vancouver Island from a westerly or northwesterly direction (Fig. 3). The sockeye salmon that were about 3,000 km or more from the Fraser River (mostly tagged in April and May) were generally distributed farther to the south than those tagged later in the season at distances from 1,000 to 2,300 km. The former must have travelled almost due east, while most of the latter may have moved northeast first and then later in the season turned southeast towards Vancouver Island.

Thus, sockeye salmon returning to the Fraser River from their ocean feeding grounds approach Vancouver Island from the west and the northwest and, depending on their homing course, generally make landfall along the west coast of Vancouver Island or farther north in Queen Charlotte Sound (Fig. 1).

West Coast Troll Fishery

To derive information on areas of landfall for different years, we used records of troll fishing off the west coast of Vancouver Island. The Canadian west coast fishery has usually been open during the period that sockeye salmon arrive on the coast. Only during 1978, 1982, 1983, and 1985 were there short nonretention periods for sockeye salmon. We assume, therefore, that in general the catches reflect the migratory patterns of these

fish in nearshore waters. The troll catches and boat efforts are recorded on a weekly basis for the different statistical areas by the Department of Fisheries and Oceans of Canada (F. Wong[3]). The west coast sockeye salmon catches generally reflect the annual variability in the total Fraser River run (Henry 1961); therefore, most sockeye salmon captured along the west coast are considered to be returning to this river. Small proportions of the catch are of Barkley Sound (Vancouver Island) and Lake Washington (USA) origin.

In 1979 and 1982 peak catches of sockeye salmon occurred near the middle of Vancouver Island in areas 24-26 (Fig. 4). The relatively low diversion rates (27 and 22% respectively during

[3]F. Wong, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada, pers. commun. 1984.

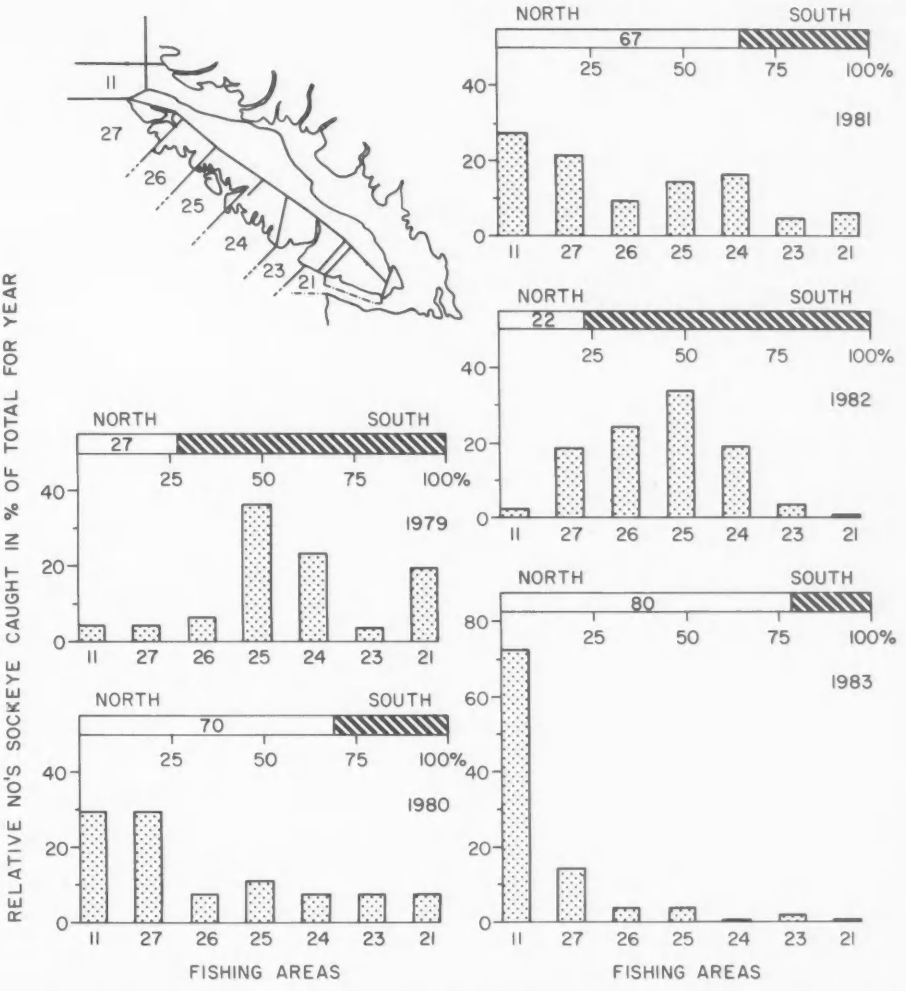


FIGURE 4.—Vertical bar graphs illustrate the proportions of the total troll catch of sockeye salmon off the west coast of Vancouver Island caught in different statistical areas (see map insert) for the years 1979-83. Horizontal bars indicate the proportions of sockeye salmon migrating to the Fraser River via the northern and southern routes.

these years) indicate that most sockeye may have migrated southwest from a relatively southerly position offshore and returned to the Fraser River via the Strait of Juan de Fuca. In 1980 and 1981 the largest sockeye catches were made near the north of Vancouver Island in areas 11 and 27 (Fig. 4). In these years 70 and 67% of the Fraser sockeye migrated through Johnstone Strait. In 1983 an extreme situation prevailed: most of the sockeye salmon were caught in area 11 (Queen Charlotte Sound) and 80% of the fish migrated via the northern route (Fig. 4).

From these results we conclude that the proportions of Fraser River sockeye salmon returning via the northern and southern routes are generally associated with the area where the fish make their landfall (see also Tully et al. 1960; Henry 1961; IPSFC 1979-1984). If the majority of Fraser sockeye approach the coast west of Vancouver Island, then most will continue to migrate via the Strait of Juan de Fuca. However, when landfall occurs north of Vancouver Island in the Queen Charlotte Sound area, most homeward migrating Fraser sockeye will travel through Johnstone Strait.

North Coast Salmon Tagging Project

During 1982 and 1983, Canada and the United States tagged sockeye salmon along the coast of northern British Columbia and southeastern Alaska to determine interception rates in the commercial fisheries of both countries near the boundary. The results of these studies provide additional information on migratory routes of this species along the North American coast. In 1982, 40,556 and in 1983, 23,052 maturing sockeye salmon were tagged in several places in southeastern Alaska and northern British Columbia (Fig. 5) (B. Riddell[4]). Most of these fish were heading for spawning rivers in southeastern Alaska and the Nass and Skeena Rivers of northern British Columbia. However, a number of sockeye salmon, 24 in 1982 and 126 in 1983, were recovered in the commercial fishery around Vancouver Island. We assume that most of these were Fraser River fish because more than 90% of sockeye salmon captured in southern British Columbia belong to Fraser River stocks.

Of the sockeye salmon tagged in the north, 9 times more were recovered in the Vancouver Island area in 1983 than in 1982 (Fig. 5), despite the fact that the total run of sockeye to the Fraser River in 1982 (13,933,000) was more than twice as large as in 1983 (5,167,000; IPSFC 1983, 1984). This indicates that in 1983 a greater proportion of Fraser River sockeye made landfall north of Vancouver Island than in 1982. This was reflected in the diversion rates through Johnstone Strait of 80 and 22% respectively for the 2 years (Figs. 1, 4). The results also show that relatively 9 (1982) to 13 (1983) times more sockeye were recovered in the Vancouver Island area from the outside (Noyes and Queen Charlotte Islands, and Cape Muzon) than from the inside (Clarence Strait and Areas 3, 4, and 5) tagging operations (Fig. 5). We suggest that the southern British Columbia sockeye primarily migrated along the west coast of the Queen Charlotte Islands during their migration south. However, some entered Dixon Entrance in 1983 and travelled through Hecate Strait towards the Fraser River, as indicated by recoveries from inside tagging locations.

The findings from the North Coast Tagging Project support the evidence presented earlier that coastal migratory routes of Fraser River sockeye can vary considerably from year to year and that during years of high diversion through Johnstone Strait the returning sockeye make landfall farther north. Analysis of catches, run timing, and stock composition led the Pacific Salmon Commission to a similar conclusion several years ago (IPSFC 1983).

In summary, our analysis of the INPFC, West Coast Troll, and North Coast Tagging data sets indicates that Fraser River sockeye salmon returning from ocean feeding grounds approach Vancouver Island from the west and northwest. The area of landfall varies yearly from the west coast of Vancouver Island to more northern regions in Queen Charlotte Sound. Moreover, the area where most salmon reach the coast is strongly correlated with the proportion that enters the Strait of Georgia via the southern or northern routes.

Migratory Routes and Oceanographic Conditions

A coastal approach north of Vancouver Island results in a higher proportion of fish moving through Johnstone Strait, while an approach farther south, along the west coast of Vancouver Island, directs the fish to the Fraser River through

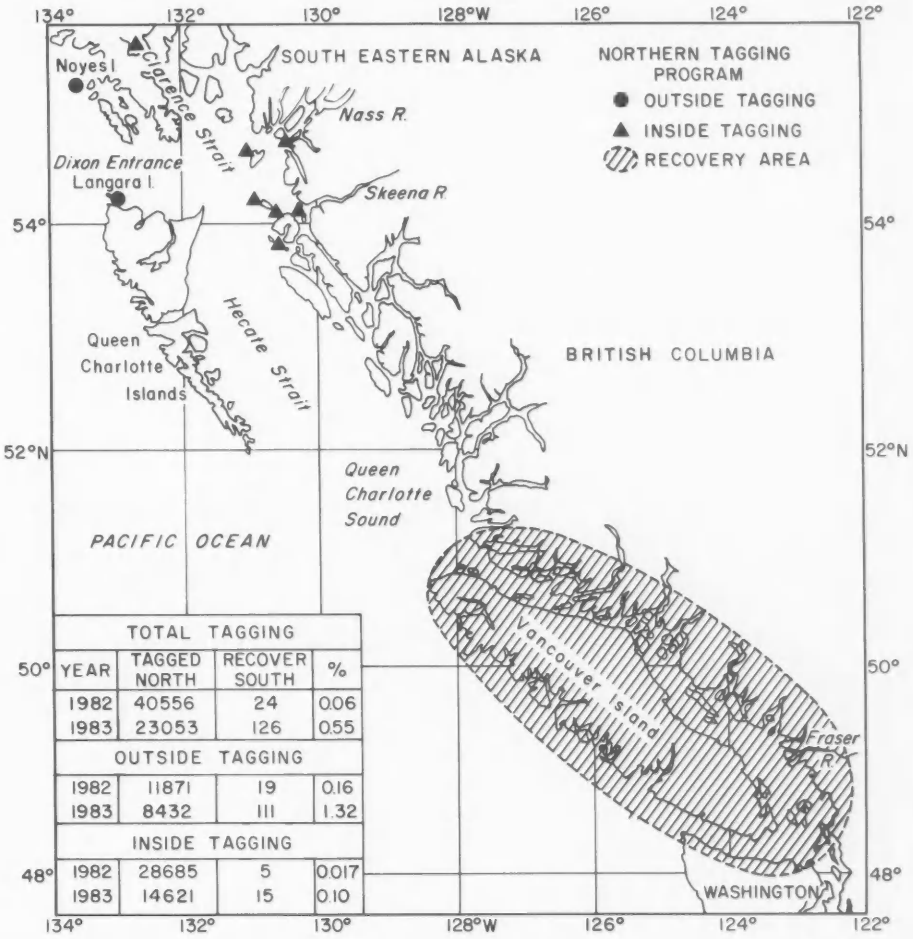
[4]B. Riddell, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada, pers. commun. 1985.

the Strait of Juan de Fuca. We propose that the coastal approach may be influenced by oceanographic conditions in the eastern Gulf of Alaska during the April-June period when the maturing sockeye perform their homing migrations from the high seas overwintering grounds to the coastal areas (French et al. 1976).

The following environmental factors were analyzed for correlation with diversion rates of Fraser River sockeye via the north:

1) Sea surface temperatures (SST) (average April-June) measured daily at four lighthouse stations along the British Columbia coast: Amphitrite Point, Kains Island, Cape Saint James, and Langara Island (Fig. 6) (Dodimead 1984; L. F. Giovando[5]). SSTs can be used as indications

[5]L. F. Giovando, Institute of Ocean Sciences, Patricia Bay, B.C. V8L 4B2, Canada, pers. commun. 1985.



TOTAL TAGGING			
YEAR	TAGGED NORTH	RECOVER SOUTH	%
1982	40556	24	0.06
1983	23053	126	0.55
OUTSIDE TAGGING			
1982	11871	19	0.16
1983	8432	111	1.32
INSIDE TAGGING			
1982	28685	5	0.017
1983	14621	15	0.10

FIGURE 5.—The numbers of sockeye salmon tagged in northern British Columbia and southeastern Alaska and recovered that year in waters around Vancouver Island. Tagging data are separated by location of tagging (inside vs. outside waters) and year (1982 vs. 1983).

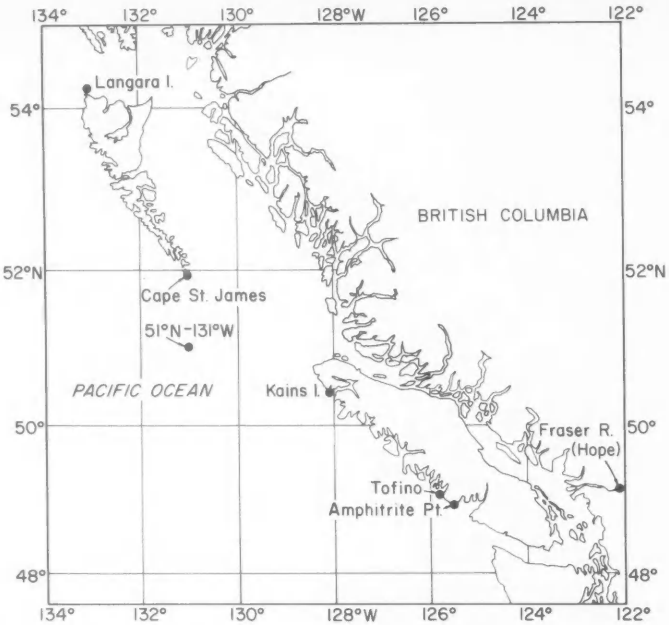


FIGURE 6.—Locations where environmental conditions were monitored for regression analysis with sockeye salmon migratory patterns: sea surface temperature and salinity at Amphitrite Point, Kains Island, Cape St. James, and Langara Island; sea level at Tofino; Ekman transport at lat. 51°N, long. 131°W; and Fraser River discharge at Hope.

of the extent of warm water intrusion from the south along the coast.

2) Sea surface temperatures (average April-June) at ocean station P (50°N, 145°W) (see Figure 8) (S. Tabata[6]) as an indication of ocean conditions in the Gulf of Alaska. After sampling at this station was terminated in 1981, temperatures for this area in the Pacific Ocean were obtained from satellite and shipboard observations.

3) Monthly mean sea-levels (average April-June) recorded at Tofino, on the west coast of Vancouver Island (Fig. 6), as an indication of convergent and divergent conditions along the coast (A. Dodimead[7]). Also, high coastal sea levels indicate northward currents.

4) Ekman transport normal to the coast (average April-June) at 51°N, 131°W (Fig. 6) calculated from barometric pressure data (Dodimead 1984; Giovando fn. 5) to indicate the general pattern of circulation from wind-driven transport.

5) Fraser River discharge (average April-June) measured at Hope (Fig. 6) (LeBlond et al. 1983; Inland Waters Directorate[8]), as an indication of coastal run-off and extent of Fraser River homewater along nearshore areas.

Linear regression analysis of Fraser sockeye diversion rates from 1953 to 1985 with SST of lighthouse data from Amphitrite Point, Kains Island, Cape St. James, and Langara Island for the months of April to June showed significant correlations (Table 1). Since the correlation coefficient of diversion rates was highest with the data from the Kains Island lighthouse, these were selected for further analysis and averaged over April, May, and June.

Regression analysis between the northern diversion rates and the environmental variables

[6]S. Tabata, Institute of Ocean Sciences, Patricia Bay, B.C. V8L 4B2, Canada, pers. commun. 1985.

[7]A. Dodimead, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada, pers. commun. 1984.

[8]Inland Waters Directorate, 1001 West Pender Street, Vancouver, B.C. V6E 2M9, Canada, 1985.

TABLE 1.—Correlations (R) of sea surface temperature at four lighthouse stations along the British Columbia coast with the percentage of sockeye salmon returning to the Fraser River via Johnstone Strait during the years 1953-83.

Lighthouse stations	March		April		May		June	
	R	*N*	R	*N*	R	*N*	R	*N*
Amphitrite Pt.	0.65	31	0.69	31	0.59	31	0.59	31
Kains Island	0.65	31	0.65	31	0.65	31	0.63	31
Cape St. James	0.54	30	0.68	29	0.66	30	0.54	30
Langara Island	0.55	31	0.62	31	0.65	31	0.64	29

TABLE 2.—Relationship (R and R^2) for linear regression analyses of average April-June SST at Kains Island lighthouse, sea level at Tofino, Ekman transport at lat. 50°N, long. 131°W, SST at Station P (50°N, 145°W), and Fraser River discharge at Hope with percentage sockeye salmon returning to the Fraser River via Johnstone Strait for the years 1953-85 ($N = 33$), 1953-77 ($N = 25$), and 1978-85 ($N = 8$). The level of significance was set at $P < 0.01$.

Factors	1953-85		1953-77		1978-85	
	R^2 (%)	R	R^2 (%)	R	R^2 (%)	R
SST Kains Island	51	0.71*	9	0.30	85	0.92*
Sea level Tofino		0.19	19	0.44	3.9	0.20
Ekman transport	4	0.29	4	−0.20	5	0.23
SST Station P	15	0.39	11	0.33	11	0.33
Fraser River discharge	2	0.14	45	0.67*	30	−0.55

*$P < 0.01$.

listed above for the years 1953-85 showed significant ($P < 0.01$) positive correlations with nearshore (Kains Island) SSTs, explaining 51% of the variance (Table 2; Fig. 7A).

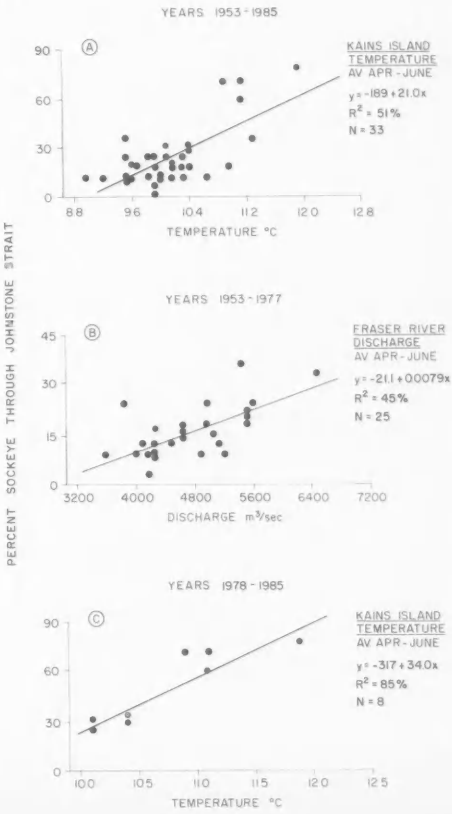


FIGURE 7.—Relationships between the proportion of Fraser River sockeye salmon migrating via the northern route (Johnstone Strait) and A) average sea surface temperature and salinity at Kains Island for April, May, and June for the years 1953-85; B) average Fraser River discharge for April, May, and June for the years 1953-77; C) average sea surface temperature at Kains Island for April, May, and June for the years 1978-85.

Inspection of the diversion rates over the last 33 years suggested that after 1977 a change occurred in the migratory patterns of Fraser River sockeye approaching the coast. During the period 1978-85, unprecedented rates of 70 to 80% have used the northern route (Fig. 1). This change in migratory behavior coincided with a remarkable prolonged warming period in the northeast Pacific Ocean (Chelton 1984; McClean 1984). The trend culminated in the extended warm-water anomaly of 1983 along the coast of British Columbia, which was associated with the 1982-83 El Niño event that occurred in the equatorial Pacific Ocean. This event was one of the most extreme of the century (Mysak 1985). We therefore carried out separate analyses for the two periods, 1953-77 and 1978-85.

The regression analyses for the 1953-77 period identified Fraser River discharge as the only significant ($P < 0.01$) factor, explaining 45% of the variance (Table 2; Fig. 7B). This positive relationship between northern diversion rates and Fraser River discharge was also suggested by Wickett (1977) for the same time period.

For the period 1978-85, the regression analyses indicated that SST at Kains Island was the only helpful predictor, explaining 85% of the variance (Table 2; Fig. 7C). A strong positive relationship between northern diversion rates of Fraser River sockeye salmon and SST at Kains Island was also noted for the years 1973-83 by staff of the Pacific Salmon Commission (IPSFC 1984).

DISCUSSION

We suggest that sockeye salmon returning to the Fraser River may have been influenced by year-to-year changes in ocean conditions during and between the periods 1953-77 and 1978-85. The relationships of sockeye migration to sea surface temperature and river discharge will be discussed separately.

Sea Surface Temperature and Sockeye Salmon Migration

Leggett's (1977) review of fish migration concluded that oceanic fish migrations largely represent the continuous optimization of physiologically important conditions. Temperature is an oceanographic feature whose importance in fish physiology is well established (Brett 1970). While evidence indicates that thermal conditions may be correlated with the timing of salmon migrations (Burgner 1980; Blackbourn in press) or the route of their return migration to coastal waters (this study), it is not clear how temperature affects salmon behavior. Temperature might directly influence salmon in some way or it might merely correlate with some other oceanographic feature influencing them such as eddies and currents (Mysak 1986), or the abundance or species composition of prey items (Fulton and LeBrasseur 1985). If so, a correlation of salmon behavior with temperature could mislead attempts to understand the control of migration.

Alternatively, temperature may indeed have a direct impact on sockeye salmon. There is considerable evidence that temperature is correlated with the distribution of marine fishes (Brett 1970; Laurs and Lynn 1977; Laurs et al. 1977; Magnuson et al. 1980). Manzer et al. (1965) and French et al. (1976) summarized the distribution of sockeye salmon in relation to sea surface temperature. While waters of certain temperatures were generally devoid of sockeye salmon, the apparent thermal preferendum was 3° to 5°C wide and changed seasonally. Manzer et al. (1965) reported that most sockeye were caught by research gill nets in the North Pacific Ocean and Bering Sea in waters of 4° to 6°C in May, 4° to 7°C in June, 8° to 12°C in July, and 9° to 12°C in August. Based on the occurrence of sockeye salmon in large areas of the North Pacific Ocean, French and Bakkala (1974) concluded that they are not exclusively associated with specific oceanic conditions.

To determine the ways in which temperature might directly affect sockeye salmon, we must ascertain the horizontal and vertical distribution of temperatures which they experience at sea on their homeward journey. An oceanographic survey of the North Pacific Ocean and Gulf of Alaska from 16 to 24 July 1959 (S.I.O.U.C. 1965) provide useful data to suit this purpose (Fig. 8). Temperatures at 0, 30, and 50 m depth were used to estimate the extent of horizontal and vertical gradients experienced by salmon migrating to the northern tip of Vancouver Island along the path which Fraser River sockeye seem to take.

If we assume that salmon swam 48 km/day on the surface along the route of the ship, they would have experienced total temperature changes of +3.68°C or a daily average of +0.10°C/day (Table 3). Averaged over the stations, vertical excursions from 0 to 30 m would have caused the fish to experience changes of −0.81°C. Dives from the surface to 50 m would have been accompanied by changes averaging −5.00°C. Earlier in the sum-

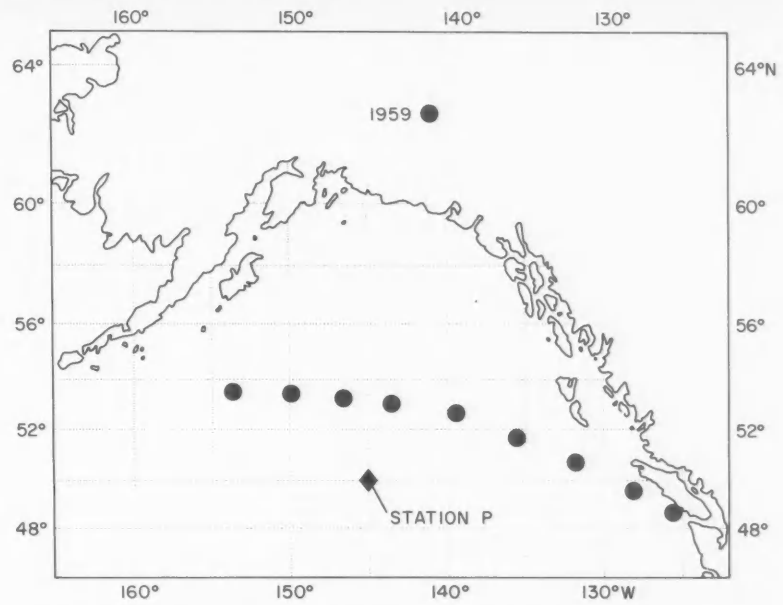


FIGURE 8.—Map of the North Pacific Ocean showing the sites sampled by an oceanographic cruise in 1959 (S.I.O.U.C. 1965) and Station P, where sea surface temperatures and salinities were also recorded.

TABLE 3.—Temperature at depth, recorded by the RV *Brown Bear*, 16-24 July 1959 (data from S.I.O.U.C. 1965).

Latitude (N)	Longitude (W)	0 m	30 m	50 m
53°56′	153°18′	10.52	9.98	4.80
53°42′	149°43′	10.54	9.49	4.60
53°30′	146°42′	10.82	9.94	4.80
52°58′	143°27′	11.20	10.90	6.82
52°18′	139°35′	10.90	10.70	6.79
51°40′	135°55′	12.39	12.12	8.58
50°40′	131°57′	13.59	10.60	8.18
49°30′	128°12′	14.20	13.96	9.59
48°44′	125°39′	[1]13.18	[1]8.90	[1]8.23

[1]Data not included in calculations of gradients.

mer when the sockeye salmon migrate through these areas, the vertical and horizontal gradients are presumably smaller.

Available information indicates that salmon in general and sockeye in particular do not restrict themselves to one depth but rather have a diel vertical movement pattern while at sea. Manzer (1964) reported that most sockeye were caught in gill nets at or near the surface during the night, but in the daytime they were caught in substantial numbers as deep as 48 to 60 m. Mishima and Shimazaki (1969) reported a more complex pattern: sockeye were most abundant on the surface at 13:00-15:00 h but a second peak of abundance occurred at 03:00-05:00 h. Whereas variations in diel movements and depth distribution may occur, it seems likely that sockeye experience temperature changes of 1°C during their daily movements, and may experience changes of 4° to 5°C if they dive below the mixed layer.

The slight changes in temperature associated with horizontal movement relative to vertical movement make it unlikely that the long-distance migration of homing sockeye is determined by physiological responses to temperature (Laevastu 1983). Moreover, the temperatures experienced by sockeye salmon at sea do not seem to reflect physiological optima (Brett 1974, 1983). Nevertheless, there is a west-east gradient of increasing temperature over much of the homeward path of Fraser River sockeye salmon. Therefore, "predictive behavioural thermoregulation" (Neill 1979) may play a role in homing, though "reactive behavioural thermoregulation" (e.g., Olla et al. 1975) probably does not. However, gradients are an inefficient aid to migration unless

coupled with an independent sense of direction. Moreover, as the salmon near the coast, they may experience a decrease in temperature (Table 3).

We conclude that the relationship between sea surface temperatures at Kains Island and the diversion rate of sockeye salmon returning to the Fraser River via Johnstone Strait between 1978 and 1985 reflects the influence of ocean conditions on the behavior of fish, either on the feeding distribution prior to homing (see also Mysak 1986) or on the homing migration itself.

Fraser River Discharge and Sockeye Salmon Migration

Most of the fresh water along the British Columbia coast originates from the Columbia, Fraser, and Skeena Rivers and distinct tongues of dilute water (SSS of 32.6‰ and less) extend seaward from the Strait of Juan de Fuca and Queen Charlotte Sound several hundred kilometers offshore (Favorite 1961). Wickett (1977) suggested that it was the Fraser River water discharged in the ocean to the northwest of Vancouver Island that increased the percentage of Fraser River sockeye migrating through Johnstone Strait.

Fraser River sockeye migrating from their ocean feeding grounds towards the British Columbia coast pass through the areas of dilute surface water ("dilute domain") long before making landfall (Fig. 9). Interannual changes in river discharge and the resulting dilute extensions offshore could affect the coastal approach routes of Fraser River sockeye by causing more northerly landfall than usual during years of high levels of runoff (Favorite 1961; Wickett 1977).

What might be the mechanism that underlies a direct relationship between river discharge and migration route of adult Fraser River sockeye salmon? Two possibilities present themselves. First, returning sockeye salmon could prefer lower salinity water as they home, similar but

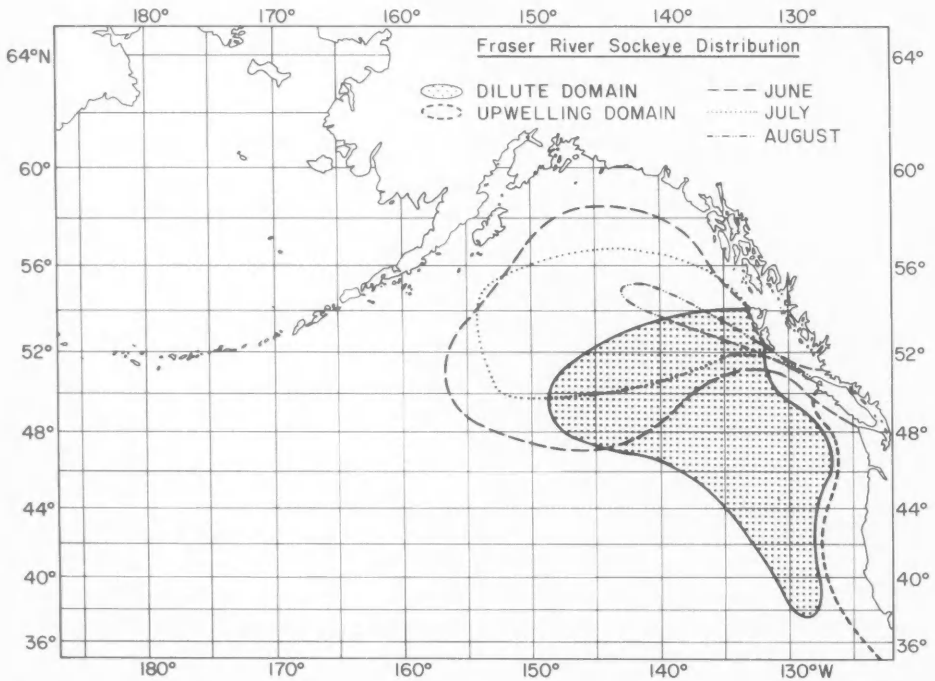


FIGURE 9.—The estimated distribution of maturing Fraser River sockeye salmon in June, July, and August in relation to regions of dilute water and upwelling.

opposite to the increasing saltwater preference documented by Baggerman (1960) and McInerney (1964) for juvenile salmon during the period of seaward migration. McInerney (1964) argued that the shift in salinity preference over time could gradually lead fish along the gradient of salinities found in coastal areas toward the open ocean.

Salinity measurements during the 1959 cruise (S.I.O.U.C 1965) mentioned previously showed that from the middle of the Gulf of Alaska to the tip of Vancouver Island, sea surface salinities decreased from 32.73 to 32.46‰ over a distance of about 1,757 km (Table 4). Fish swimming at a rate of 48 km/day would have met changes averaging 0.00015‰/km or 0.0074‰/day when approaching the coast. The threshold for recognition of salinity differences by sockeye salmon is unknown. However, if it is similar to that of minnows (*Phoxinus phoxinus*) of 0.003‰ (Glaser 1966), then it is about 20 times higher than the average difference that wil be encountered during a km of travel.

TABLE 4.—Salinity at depth, recorded by the RV *Brown Bear*, 16-24 July 1959 (data from S.I.O.U.C. 1965)

Latitude (N)	Longitude (W)	0 m	30 m	50 m
53°56′	153°18′	32.73	32.84	32.88
52°42′	149°43′	32.75	32.84	32.88
53°30′	14€°42′	32.85	32.86	32.95
52°58′	143°27′	32.60	32.61	32.72
52°18′	139°35′	32.66	32.68	32.83
51°40′	135°55′	32.24	32.31	32.53
50°40′	131°57′	32.15	32.31	32.57
49°30′	128°12′	32.46	32.47	32.53
48°44′	125°39′	[1]31.35	[1]32.28	[1]32.73

[1]Data not included in calculations of gradients.

Moreover, salinity changes towards the coast do not occur in a smooth gradient (Table 4). Water masses of different salinities and temperatures form a dynamic patchwork that is continuously changing under the influence of wind and currents (Tabata 1984). We therefore consider it unlikely that a general preference for lower salinity water determines the approach direction of homing Fraser River sockeye migration. Smith (1985) concluded that for fishes in general ". . .there is little evidence that salinity is a guiding mechanism."

Second, the sockeye could react to home odors from the Fraser River in the offshore waters as suggested by Favorite (1961) and Wickett (1977). The sensitivity of salmonids to certain odors is high: 10^{-8} M for morpholine and 10^{-9} M for free amino acids (Brett and Groot 1963; Hara et al. 1984). However, it is questionable that, given the extensive mixing in the Fraser River and in the ocean, the already low concentrations of odors from the different nursery lakes would be above threshold. Moreover, odors generally act as releasers and not as directors of responses (Johnsen and Hasler 1980). It is difficult to understand how salmon could change their migration routes far offshore in the ocean, even if they could sense the aroma of their home water. We therefore conclude that the relationship between Fraser River discharge and diversion rate of sockeye salmon returning via the northern route is not a direct, but probably an indirect one.

CONCLUSION

We hypothesize that Fraser River discharge (1953-77) and SST at Kains Island (1978-85) primarily reflect certain atmospheric and related oceanographic conditions, which affect Fraser River sockeye salmon winter distribution and/or migration in the ocean. The weather conditions in the Gulf of Alaska are controlled by the locations and intensities of two major semipermanent atmospheric pressure cells; the Aleutian low and the North Pacific high (Favorite et al. 1976; Thomson 1981; Emery and Hamilton 1985). The interannual variations of these pressure cells affect precipitation and the extent of the snow pack during the winter, as well as temperature, salinity, and circulation patterns in the ocean (Favorite et al. 1976; Thomson 1981; Emery and Hamilton 1985).

Anomalous temperature conditions in the ocean, resulting from varying atmospheric conditions, may affect salmon migrations directly or indirectly by acting on their feeding distribution or on the distance or direction they must travel to reach home. When ocean conditions are warmer than usual, sockeye salmon tend to encounter the coast of British Columbia at the north of Vancouver Island. In such cases their approach to the Fraser River will be primarily through Johnstone Strait. Following cold winter conditions in the Gulf of Alaska, landfall usually occurs along the west coast of Vancouver Island and migration to the home river is primarily via the Strait of Juan de Fuca.

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PREDATION ON *CAPITELLA* SPP. BY SMALL-MOUTHED PLEURONECTIDS IN PUGET SOUND, WASHINGTON[1]

D. SCOTT BECKER[2] AND KENNETH K. CHEW[3]

ABSTRACT

This study examined the predation patterns of three flatfishes (English sole, Dover sole, and rex sole) on the opportunistic polychaetes *Capitella* spp. in disturbed soft-bottom habitats of Puget Sound, Washington. Sampling was conducted throughout the diel cycle during May and June 1981. All three fishes exhibited some degree of selective predation on *Capitella* spp. based on both number and size of these prey. Numerical dietary contribution by *Capitella* spp. was greatest at night for all three fishes, suggesting that these polychaetes become more accessible to predators at night. Predation on *Capitella* spp. allowed English sole to alter their normal diurnal feeding chronology and forage successfully at night. This study supports the hypothesis that some demersal fishes can exploit opportunistic prey in disturbed habitats.

The composition of soft-bottom marine benthic invertebrate assemblages can be altered by a variety of natural and anthropogenic disturbances, including salinity reduction (Boesch et al. 1981), storm-induced surge (Rees et al. 1977), hypoxia (Santos and Simon 1980), dredge-spoil dumping (Rhoads et al. 1978), sewage disposal (Pearson and Rosenberg 1978), and oil spills (Sanders et al. 1980). To predict the effects of these events on demersal fishes, predator-prey relationships between benthic invertebrates and their piscine predators must be understood. Unfortunately, this kind of information is rare for marine ecosystems (Mills 1975).

Frequently, benthic invertebrate assemblages in disturbed habitats are dominated by one or more opportunistic species (e.g., Grassle and Grassle 1974; McCall 1977; Pearson and Rosenberg 1978; Rhoads et al. 1978). These opportunists are adapted to rapidly colonize disturbed environments and often attain exceptionally high population densities. Because many of these species reside at or near the sediment-water interface, they represent a potential food bonanza to bottom-feeding demersal fishes. When fishes encounter such an abundant and accessible food source, it seems likely that those species capable of modifying their foraging behavior to fully exploit this windfall will do so. Such opportunistic predation on temporally or spatially variable superabundant prey has been found for a variety of fishes (e.g., Nilsson 1960; Ivlev 1961; Zaret and Rand 1971; Murdoch et al. 1975), and is one prediction of optimal foraging theory (review in Pyke et al. 1977).

As an example of how a group of demersal fishes responds to a disturbed soft-bottom habitat dominated by opportunistic benthic invertebrates, we describe the foraging patterns of three flatfishes (Pleuronectidae) in Puget Sound, WA on *Capitella* spp., a well-known group of opportunistic polychaetes (Grassle and Grassle 1974; Pearson and Rosenberg 1978). The flatfishes targeted for study were English sole, *Parophrys vetulus*; Dover sole, *Microstomus pacificus*; and rex sole, *Glyptocephalus zachirus*. These fishes belong to the small-mouthed subgroup of pleuronectids identified by Moiseev (1953) and, as such, prey primarily upon small infaunal and epifaunal benthic invertebrates. These species also form a major component of demersal fish assemblages in Puget Sound (Miller et al. 1977; Wingert and Miller 1979; Becker 1984), as well as in most nearshore areas along the west coasts of the United States and Canada (e.g., Alverson et al. 1964; Day and Pearcy 1968; Hart 1973; Allen 1982).

MATERIALS AND METHODS

Field Sampling

The study was conducted on the delta of the

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Puyallup River, in Puget Sound's Commencement Bay (Fig. 1). This dynamic area receives a variety of anthropogenic and natural discharges. For example, the river discharges approximately 5,500 kg/year of sediments in a seasonally variable manner (Dexter et al. 1981). In addition, the City of Tacoma releases primary-treated sewage into the river at an annual flow rate of 0.9 m^3/second (20.5 MGD) approximately 2.4 km upstream from the river mouth (Tetra Tech 1981). A preliminary survey conducted by the authors showed that benthic invertebrate assemblages throughout much of the delta were dominated numerically by *Capitella* spp.

Field sampling was conducted from 26 May to 3 June 1981. All three target species have spawned by this time (Hart 1973) and, as typical of most adult pleuronectids, are presumably feeding intensely to replenish the energy used previously for migration, overwintering, and spawning (e.g., Moiseev 1953; Roff 1982).

Sampling was conducted along two 300 m transects located at a depth of 32 ± 2 m (Fig. 1). This depth corresponds to the upper boundary of the

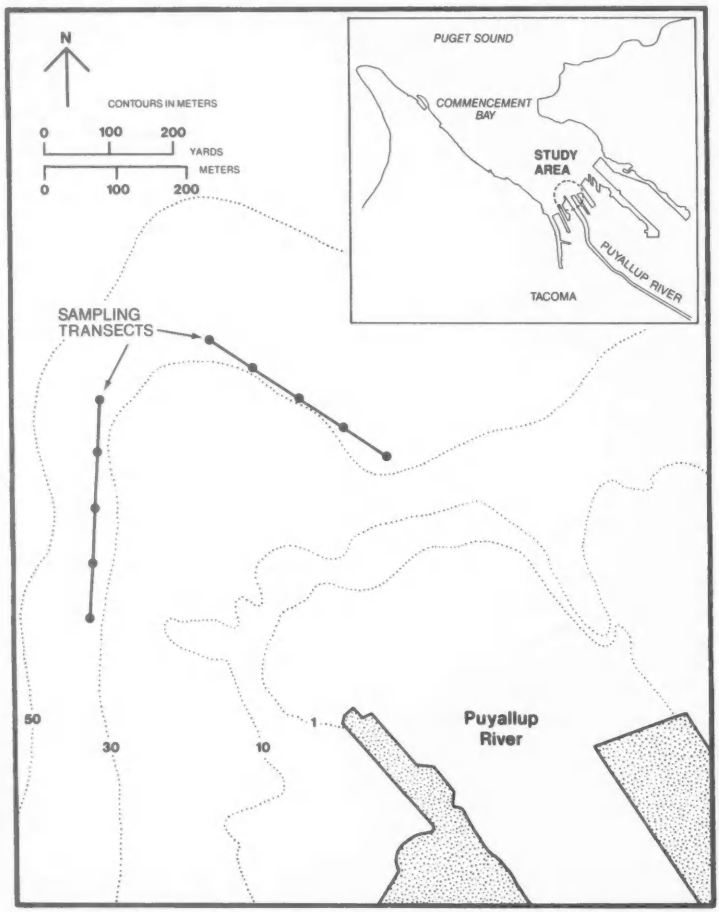


FIGURE 1.—Locations of sampling transects and benthic sampling points (i.e., large dots) along each transect.

intermediate faunal zone (i.e., 30-70 m depth) identified for Puget Sound demersal fish assemblages by Wingert and Miller (1979). All three target species are sufficiently abundant in this depth zone to allow a quantitative food habits analysis to be conducted. Data from both transects were pooled prior to analysis.

Fishes were collected using a 7.6 m (headrope) otter trawl having a body mesh size of 3.2 cm (stretched) and a cod-end liner mesh size of 0.8 cm (stretched). Trawling was conducted along both transects at a constant vessel speed of approximately 2.5 kn. All positioning was achieved using the LORAN-C navigation system. To assess diel variations in feeding behavior, hauls were made along each transect during four periods of the diel cycle: morning (0900-1030 h), afternoon (1300-1500 h), evening (1900-2030 h), and night (2330-0100 h). Each transect was sampled twice during each time period, yielding eight hauls per transect or a total of 16 hauls for the study.

At sea, the stomach contents of the target species were fixed by injecting, using a 50 cc syringe, a 10% solution of buffered formalin into the body cavity of each individual. These fishes were then brought to the laboratory and stored at 4°C.

Benthic invertebrates along each transect were sampled within 2 days of trawling. Organisms were collected using a 0.1 m^2 van Veen bottom grab, sieved through a 1.0 mm mesh screen, fixed with a 10% solution of buffered formalin, and transferred to 70% ethanol for storage. A single grab sample was taken during daytime at each of five sampling points positioned at approximately equal distances along each transect (Fig. 1).

Laboratory Analysis

Within 5 days of sampling, the total length (TL) of each fish was measured to the nearest 1.0 mm. The body cavity was then opened and the stomach was removed by severing the esophagus and pylorus. Stomachs were stored in 70% ethanol prior to analysis.

For food habits analysis, stomachs were subsampled from the total pool of available stomachs. To minimize within-species variation as a result of size-dependent foraging patterns (e.g., Gabriel and Pearcy 1981), only individuals within an 80 mm length range were selected for analysis. The ranges used for English sole, Dover sole, and rex sole were 240-320, 200-280, and 210-290 mm TL, respectively. Each length range bracketed the median length observed for each species.

Identifications of all invertebrates in stomachs and benthic samples were made using a dissecting microscope. Sizes of all *Capitella* spp. were estimated using the width of the fifth setiger (cf. Tsutsumi and Kikuchi 1984). This measurement was used instead of body length because many of these polychaetes were fragmented during grab sampling or ingestion by the fishes. Setiger widths were measured to the nearest 0.1 mm using an ocular micrometer.

The dietary contribution of *Capitella* spp. to the total stomach contents of each target species was estimated using percentages based on numerical proportions. In addition, the total number of prey per stomach (i.e., *Capitella* spp. plus all other organisms) was used as an index of feeding intensity for each species.

Statistical Analysis

Nonrandom predation on *Capitella* spp. (i.e., selection) was tested by comparing the numerical proportions of these polychaetes in the stomachs of the fishes with the proportion found in the benthos using a 2×2 contingency formulation and the chi-square criterion (Pearre 1982). Direction of selection was determined by inspecting the relative proportions of prey in the stomachs and benthos. Nonrandom size selection of *Capitella* spp. was tested by comparing the size distributions of these polychaetes in the stomachs of the fishes with the size distribution found in the benthos using the Mann-Whitney U-test. In both of these analyses, four comparisons (i.e., one for each time period) for each species were made with a single set of benthic observations. Because these four comparisons lacked independence, significance levels were adjusted conservatively using Bonferroni's technique (Miller 1981).

To examine how the foraging patterns of English sole differed between habitats where benthic assemblages were dominated by *Capitella* spp. and habitats where assemblages did not include these polychaetes, the values of feeding intensity (i.e., numbers of prey per stomach) found in the present study were compared with those obtained at six other sites in Puget Sound by Becker (1984). These six sites were located at depths between 12 and 32 m, and fishes were sampled and processed using methods identical to those described for the present study. Values of feeding intensity were compared during each period of the diel cycle using the Mann-Whitney U-test. Similar analyses could not be conducted for Dover

sole and rex sole because these fishes were not sufficiently abundant at the six additional sites.

RESULTS

Prey Selection

Throughout the diel cycle, the numerical proportion of *Capitella* spp. in the diets of all three fishes exceeded the proportion of these polychaetes in the benthos (Table 1). Selection of *Capitella* spp. was highly significant ($P < 0.001$) during all four time periods for English sole and rex sole, and during morning and night for Dover sole. Selection was significant at $P < 0.01$ during evening for Dover sole, but not significant ($P > 0.05$) during afternoon for this species.

TABLE 1.—Comparisons of proportions of *Capitella* spp. in fish stomachs with the proportion in the benthos using a 2 × 2 contingency test. **P < 0.01, ***P < 0.001, ns = P > 0.05 (experimentwise).

	Number of *Capitella* spp./Total number of prey[1,2]			
Species	Morning	Afternoon	Evening	Night
English sole	508/1,464*** (50)	425/1,029*** (40)	1,072/1,596*** (32)	1,904/2,592*** (56)
Dover sole	329/861*** (35)	114/416 ns (21)	200/612** (36)	218/461*** (36)
Rex sole	456/526*** (16)	272/412*** (18)	209/276*** (15)	603/671*** (19)

[1]Number of stomachs examined is given in parentheses.
[2]Proportion of *Capitella* spp. in the benthos was 904/3,517.

Percent numerical contribution by *Capitella* spp. to the total diet varied considerably among the three fishes (Fig. 2). Rex sole showed the greatest preference for these polychaetes, including them in 66-90% of the diet throughout the diel cycle. By contrast, Dover sole exhibited the least preference for *Capitella* spp., including them in only 27-47% of the diet. English sole showed moderate preference for these polychaetes, including them in 35-73% of the diet. Diel variation of feeding intensity closely paralleled dietary contributions of *Capitella* spp. for English sole and rex sole, with both variables peaking at night (Fig. 2). For Dover sole, however, these two variables followed substantially different diel trends, with percent dietary contribution of *Capitella* spp. reaching its maximum and feeding intensity dropping to its minimum at night.

Although the magnitudes of percent dietary contribution by *Capitella* spp. differed among the three fishes, several similarities existed in the diel variation of these values (Fig. 2). Minimum dietary contributions were found during morning (English sole) or afternoon (Dover sole and rex sole), whereas maximum contributions were found at night (all three fishes).

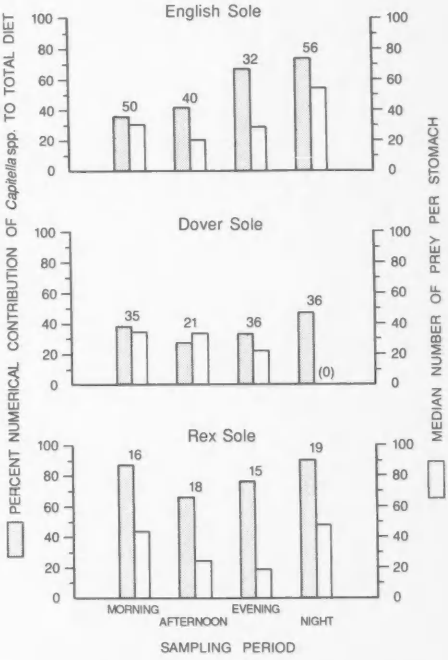


FIGURE 2.—Diel predation patterns of the target species. Number of stomachs examined is presented above each pair of bars.

Prey Size Selection

Median size of *Capitella* spp. in stomachs exceeded the median size of these polychaetes in the benthos during all four time periods for English sole and rex sole, and during morning, afternoon, and night for Dover sole (Fig. 3). Median prey size for Dover sole during evening was approximately equal to median size of *Capitella* spp. in the benthos. Size differences of *Capitella* spp. between diets and the benthos were highly significant ($P < 0.001$) during all four time periods for rex sole, during morning, afternoon, and night for English sole, and during morning and afternoon for Dover sole. Size differences were significant at

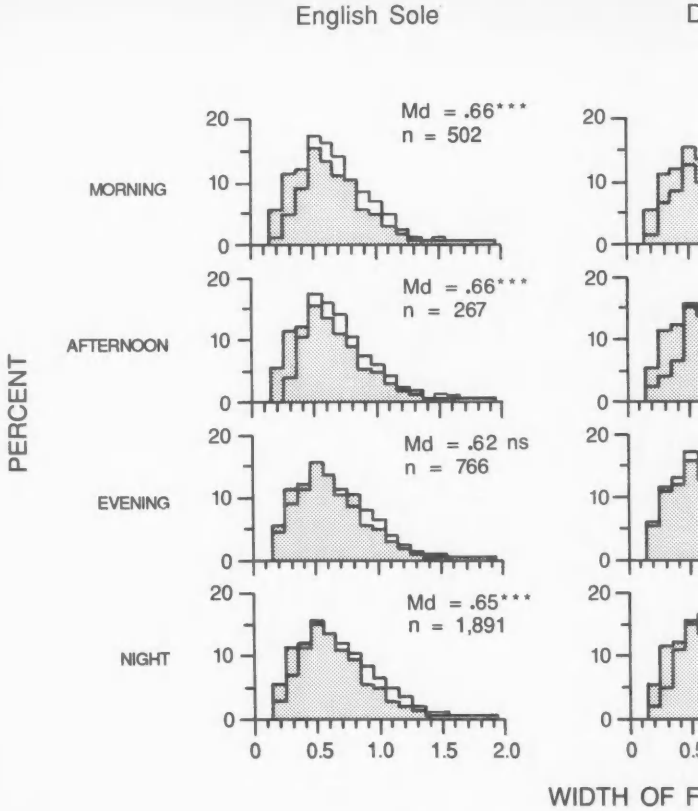
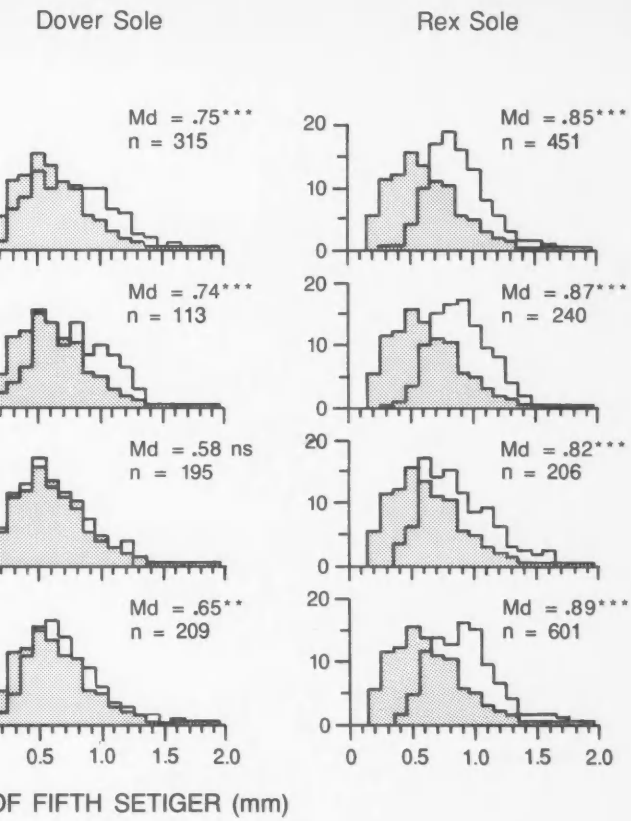


FIGURE 3.—Comparisons of size distributions of *Capitella* spp. in fish stomachs (i.e., open distributions) with the size distribution in the benthos (i.e., stippled distribution) using the Mann-Whitney U-test. Median size (Md) and sample size (n) are given with each



each distribution from the stomachs. Median size in the benthos was 0.59 mm and sample size was 898 individuals. $^{**}P < 0.01$, $^{***}P < 0.001$, ns = $P > 0.05$ (experimentwise).

$P < 0.01$ during night for Dover sole. No significant size differences ($P > 0.05$) were found during evening for English sole and Dover sole.

Of the three fishes, rex sole selected the largest *Capitella* spp. during every time period, with median size ranging from 0.82 to 0.89 mm throughout the diel cycle. Median size of *Capitella* spp. selected by English sole and Dover sole ranged from 0.62 to 0.66 mm and 0.58 to 0.75 mm, respectively.

Habitat Comparisons

Differences in number of prey per stomach between English sole captured in habitats where *Capitella* spp. were present and conspecifics captured in habitats where these polychaetes were absent were highly significant ($P < 0.001$) at night, but not significant ($P > 0.05$) during morning, afternoon, and evening (Fig. 4). The diel trends of feeding intensity in the two habitats were strikingly different. Where *Capitella* spp. were present, feeding intensity increased from afternoon to evening, and then peaked at night (median = 53.5 prey per stomach). By contrast, in habitats where *Capitella* spp. were absent, feeding intensity declined from afternoon to evening, and reached a minimum (median = 0 prey per stomach) at night.

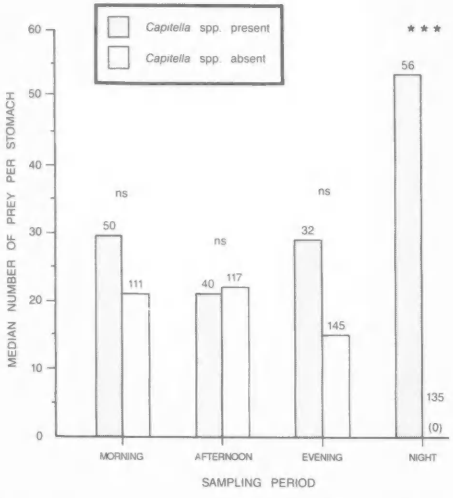


FIGURE 4.—Comparisons of values of feeding intensity for English sole between habitats with and without *Capitella* spp. using the Mann-Whitney U-test. Number of stomachs examined is presented above each bar. Significance level is given above each pair of bars. ***P < 0.001, ns = P > 0.05.

DISCUSSION

Although *Capitella* spp. accounted for only 25.7% of benthic individuals, their importance as prey to English sole, Dover sole, and rex sole was substantial. All three fishes exhibited significant ($P < 0.05$) numerical and size selection of these polychaetes during all or most of the diel cycle. Based on literature accounts of the food habits of these fishes, the observed importance of *Capitella* spp. as prey could not have been predicted directly.

Most historical accounts of the food habits of the three fishes do not identify *Capitella* spp. as prey (e.g., Hagerman 1952; Kravitz et al. 1977; Hulberg and Oliver 1978; Pearcy and Hancock 1978; Gabriel and Pearcy 1981; Allen 1982; Hogue and Carey 1982). However, most of these studies were conducted in areas where *Capitella* spp. generally would not be expected to occur in large numbers in the benthos (i.e., the continental shelf off Oregon and California). At least two studies have found that one or more of these fishes consume *Capitella* spp. Cross et al. (1984) examined the food habits of English sole ($n = 13$) and Dover sole ($n = 38$) in areas influenced by sewage discharges off Los Angeles, CA. Although *C. capitata* numerically accounted for 40-95% of benthic assemblages, the dietary contributions by this polychaete were small (i.e., 0% for English sole and <10% for Dover sole). Toole (1980) found that *C. capitata* was a major prey item of juvenile English sole (66-102 mm TL, $n = 45$) captured on an intertidal sand flat in Humbolt Bay, CA. However, because benthic assemblages were not sampled, it is unknown whether these fish were preying nonrandomly on *C. capitata*.

Of the three fishes sampled in the present study, rex sole exhibited the greatest degree of selective predation on *Capitella* spp. This species was the only one to nonrandomly select *Capitella* spp. based on both prey number and prey size throughout the diel cycle. In addition, rex sole selected the largest *Capitella* spp. of the three fishes, and included these polychaetes in the largest percentage of total diet during all four time periods. The observed peak in feeding intensity at night agrees with past descriptions of rex sole as a nocturnal forager (Kravitz et al. 1977; Allen 1982; Becker 1984). The concomitant peak in percent dietary contribution of *Capitella* spp. at

night indicates that when rex sole were feeding most intensely, selection of *Capitella* spp. was at its highest level.

Dover sole was the least selective of the three fishes with respect to predation on *Capitella* spp. This species did not exhibit selective predation based on prey number during afternoon, nor based on prey size during evening. In addition, the percent dietary contribution by *Capitella* spp. for Dover sole was the smallest of the three fishes during three of the four time periods. The observed minimum level of feeding intensity at night is consistent with the description of Dover sole as a diurnal forager (Allen 1982; Becker 1984). The nighttime peak in percent dietary contribution by *Capitella* spp. suggests that even though this fish normally does not forage at night, *Capitella* spp. could be captured quite successfully relative to other benthic invertebrates.

English sole was intermediate between rex sole and Dover sole with respect to degree of selective predation on *Capitella* spp. Although this species selectively consumed these polychaetes based on prey number throughout the diel cycle, prey size selection was not observed during evening. In addition, dietary contribution by *Capitella* spp. for English sole was the smallest of the three fishes during morning, but intermediate in magnitude during the remainder of the diel cycle. The observed peak in feeding intensity at night is contradictory to the description of English sole as a diurnal forager (Allen 1982; Hogue and Carey 1982; Becker 1984). Because dietary contribution of *Capitella* spp. peaked at a high level of 73% at night, much of the ability of English sole to forage at night resulted from predation on these polychaetes. The influence of *Capitella* spp. on nocturnal foraging by English sole was confirmed by the comparison of diel variation of feeding intensity in habitats with and without *Capitella* spp.

The observed diel variations of predation on *Capitella* spp. could have resulted from behavioral differences of either the fishes or the polychaetes. Because the fishes were sampled throughout the diel cycle, much of the variation due to the predators was accounted for. However, because diel variation in behavior of *Capitella* spp. could not be evaluated using the sampling methods employed in this study, variation in prey availability is unknown. However, at least one pattern is suggested. Because dietary contribution by *Capitella* spp. peaked at night for all three fishes, these polychaetes may become more active at the sediment surface and thus more vulnerable to predation at night. The ability of English sole to alter its normal diurnal feeding chronology to forage primarily on *Capitella* spp. at night further suggests that these polychaetes become more accessible at night. Levinton (1971) found that the bivalve *Macoma tenta* foraged primarily at night and suggested that this periodicity was used, in part, to avoid diurnal predators (primarily winter flounder, *Pseudopleuronectes americanus*). Although this defense mechanism may succeed with obligate diurnal predators, it would not be effective in avoiding nocturnal predators (e.g., rex sole) or species capable of modifying their normal diurnal feeding chronology (e.g., English sole).

From an applied standpoint, results of this study have several implications regarding the concept of disturbance management described by Rhoads et al. (1978). Those authors suggested that by properly managing habitat disturbance (i.e., dredge-spoil disposal in their case), benthic invertebrate assemblages can be maintained in the early successional stages when they are dominated by pioneering species, including opportunists such as *Capitella* spp. Because productivity of these early successional stages generally exceeds that of later stages, Rhoads et al. (1978) hypothesized that benthic assemblages dominated by pioneering species represent an enhanced food resource for demersal fishes. The observed importance of *Capitella* spp. as prey for the three fishes considered in the present study supports this hypothesis. For example, all three fishes selectively preyed upon *Capitella* spp. throughout all or most of the diel cycle, and English sole was able to modify its normal diurnal feeding chronology to prey primarily on these polychaetes at night.

Although the hypothesis of Rhoads et al. (1978) is supported by the present study, enhancing the productivity of a food resource may not be beneficial to demersal fishes if the nutritional quality of their diet is reduced in the process. For example, a variety of fish diseases have been attributed, in part, to dietary deficiencies or imbalances of specific nutrients (reviews in National Research Council 1977, 1981). In addition, the toxicity of chemical contaminants to fishes may be enhanced as a result of improper diets (e.g., Mehrle et al. 1977). Although *Capitella* spp. accounted for only 25.7% of the benthic invertebrates sampled in the present study, the dietary contributions of these polychaetes generally were much greater, especially for rex sole. Given the influence of a balanced diet on fish health, it is possible that pro-

longed dietary restriction to one or several opportunistic prey could compromise the health of the fishes.

In summary, all three fishes exhibited some degree of selective predation on *Capitella* spp. based on both number and size of these prey. Dietary contribution by these polychaetes was greatest at night for all three fishes, suggesting that *Capitella* spp. may become more accessible to predators at night. Predation on *Capitella* spp. allowed English sole to alter its normal diurnal feeding behavior and forage successfully at night. Finally, this study supports the hypothesis that some demersal fishes can exploit opportunistic prey in disturbed habitats.

ACKNOWLEDGMENTS

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THE REPRODUCTIVE BIOLOGY OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, IN THE BERING SEA, WITH REFERENCE TO SPAWNING STOCK STRUCTURE

SARAH HINCKLEY[1]

ABSTRACT

The reproductive biology of walleye pollock, *Theragra chalcogramma*, in the Bering Sea was studied from collections of ovaries and observations of spawning in 1984. Spawning occurred in the Aleutian Basin from January through March, in the southeastern Bering Sea from March through June, and northwest of the Pribilof Islands from June through August. Spawning concentrations found in these areas showed significant differences in length at age and fecundity. Histological evidence indicated that the spawning period of an individual female probably lasts less than 1 month. Results indicate at least three separate spawning stocks of walleye pollock within the Bering Sea. These are located in the Aleutian Basin, over the southeastern continental shelf and slope and northwest shelf areas, and over the continental slope northwest of the Pribilof Islands. Mixing of stocks between widely separated spawning grounds due to extended spawning and migration is not likely.

Walleye pollock, *Theragra chalcogramma*, a member of the gadid family found in the North Pacific Ocean, currently supports the largest single-species fishery in the world. In the eastern portion of its range, catches of pollock average 100,000 to 300,000 metric tons (t) per year in the Gulf of Alaska (Alton et al. in press) and 1,000,000 t per year in the Bering Sea (Bakkala et al. in press). The walleye pollock resource in the Bering Sea is presently managed as a single stock but there is increasing evidence that substocks may exist (Lynde et al. 1986[2]). If substocks exist, this information should be considered in management strategy.

If a stock is defined as a production unit or a group of fish showing similar responses to environmental conditions within a certain geographic area, then population characteristics such as growth rates, fecundity, and size or age at maturity may provide the most practical means of differentiating these units. As these parameters determine the yield of a stock to a fishery, identification of production units based on some or all of them may improve the effectiveness of fisheries management.

A clearer understanding of the reproductive process in walleye pollock may also aid in differentiating stocks or production units. Nishiyama and Haryu (1981) proposed that walleye pollock in the Bering Sea may migrate and spawn over extensive distances during the long spawning season, implying that spawning groups mix over large areas. Sakurai (1982) has shown in laboratory experiments that walleye pollock spawn a single group of matured eggs in successive batches, possibly over a period of 1 month. It is not known, however, whether an individual female is capable of repeating vitellogenesis with more than one separate group of eggs in 1 year (i.e., of rematuring the ovary). Evidence of batch spawning or rematuration in Bering Sea walleye pollock may indicate the duration of individual spawning and the potential for mixing between spawning concentrations found in widely separated areas.

In this study, the spatial and temporal distribution of spawning for 1984 has been documented and the length at age and fecundity of walleye pollock from spawning concentrations in different areas has been determined. Walleye pollock ovaries were examined histologically to clarify the process of oocyte development, to learn whether annual fecundity is determinate or indeterminate and to learn the optimal stage for estimating fecundity, and to determine whether

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

[2]Lynde, C. M., M. Van Houghton Lynde, and R. C. Francis. 1986. Regional and temporal differences in growth of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea and Aleutian Basin with implications for management. NWAFC Proc. Rep. 86-10. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

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batch spawning or rematuration occur in Bering Sea pollock.

METHODS

Data and Sample Collection

Data and specimens of walleye pollock were collected from December 1983 to October 1984 by National Marine Fisheries Service (NMFS) observers aboard foreign commercial fishing vessels and by NMFS pesonnel aboard NOAA research vessels. Data collection was divided into three phases. First, fisheries observers logged the time and location of commerical hauls in which spawning walleye pollock (those with running eggs or milt) were observed. A total of 1,538 observations was made between January and October. Second, otoliths were collected from walleye pollock in hauls where spawning was observed. Third, walleye pollock ovaries were collected for histology and anaylsis of fecundity. Three ovaries per maturity stage (Hinckley 1986) were collected and preserved in 10% neutral buffered formalin for histological analysis. A separate collection of late developing or mature ovaries was made for the fecundity analysis. Five ovaries per 5 cm length interval were collected over the entire length range encountered. These ovaries were preserved in modified Gilson's solution (Ito 1977[3]). A total of 345 ovaries were collected for histology and 294 for fecundity analysis.

Data and Sample Processing

Location of Spawning and Length at Age of Spawners

Spawning locations of walleye pollock were plotted by month. The distribution of fishing effort by the foreign commercial fleet over the spawning season was examined and compared with locations where spawning was found. Water temperatures and depths of capture at spawning locations were also examined.

For the length-at-age analysis, five areas were defined within the Bering Sea based on oceanographic features (after Lynde et al. fn. 2): the southeast continental shelf, the southeast continental slope, the northwest shelf, the northwest slope, and the Aleutian Basin (Fig. 1). Northwest and southeast areas were divided at the Pribilof Islands and buffer zones were defined in order to clearly separate them. Ages were assigned to a maximum of 200 otoliths per area by readers at the Northwest and Alaska Fisheries Center (NWAFC) age and growth laboratory.

Lynde et al. (fn. 2) found that walleye pollock from the Aleutian Basin and the northwest slope were generally slower growing than pollock from the southeast shelf and slope areas. Based on this observation, R. Francis and A. Hollowed[4] classified walleye pollock as "northern" (slow-growing) or "southern" (fast-growing), and developed two corresponding growth curves. In the present study, the growth of walleye pollock from spawning concentrations in different areas was compared to the two growth curves described in Francis and Hollowed's unpublished study. The geographical distribution of the two growth types was then examined.

To derive their "northern" and "southern" growth curves, Francis and Hollowed (unpubl. data) used age data collected by foreign fisheries observers from 1978 to 1983. Age samples were separated into $\frac{1}{2}^{\circ}$ latitude by 1° longitude cells. The mean length at age was estimated for each cell by year, quarter, and sex.

Estimates of mean length at age for each cell were used to classify the cell as "northern", "southern", or "unknown". The "northern" classification indicated that the distribution of mean length at age in a given cell was similar to that seen by Lynde et al. (fn. 2) in the northwest slope and Aleutian Basin areas (Fig. 1). The "southern" classification indicated that growth was similar to that observed by Lynde et al. (fn. 2) in the southeast slope and shelf areas (Fig. 1).

For this classification, the von Bertalanffy (1938) growth model was fitted to the weighted mean length-at-age data for the "northern" and "southern" areas for each quarter and sex over a period of 6 years (1978-83) (Lynde et al., fn. 2). The model was fitted using the BMDP PAR derivative-free nonlinear least squares estimation procedure (Dixon 1983) to produce predicted mean lengths at age for "northern" and "southern" fish.

[3]Ito, D. H. 1977. Fecundity of the copper rockfish, *Sebastes caurinus* (Richardson), from Puget Sound, Washington. Unpubl. manuscr. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

[4]Robert Francis and Anne Hollowed, Northwest and Alaska Fisheries Center, National Marine Fisheries Service NOAA, 7600 Sand Point Way N.E, Seattle, WA 98115, pers. commun. January 1985.

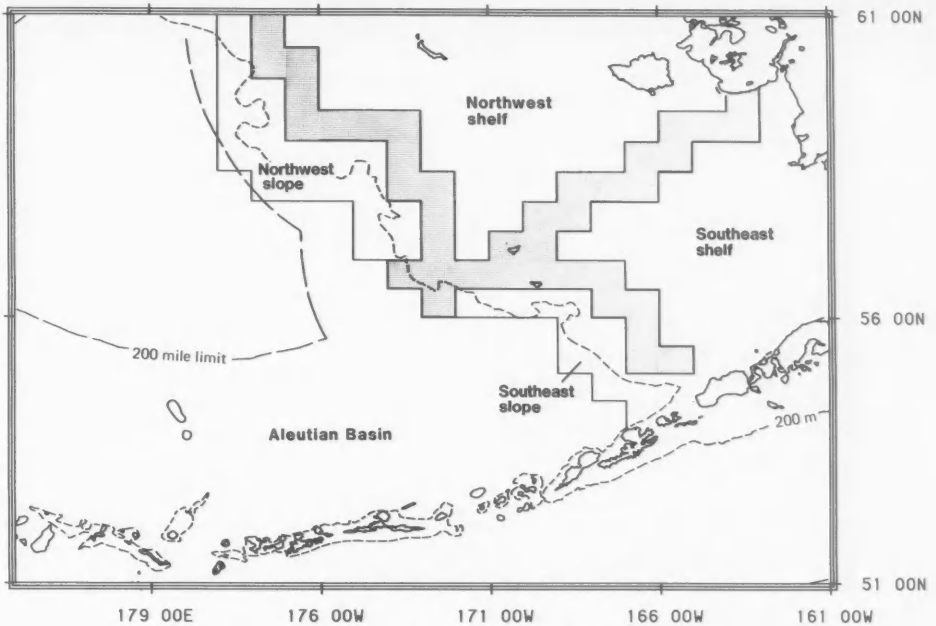


FIGURE 1.—Sampling areas within the Bering Sea. Shaded areas are buffer zones.

The cells were then classified for each sex and quarter using an index of similarity, $Pr(s)$. This index was based on the ratio of the sum of squared deviations of the observed mean length at age from the 6-yr fitted average for the southern region, to the sum of the squared deviations of the observed mean length at age from the southern and northern regions combined:

$$Pr(s) = 1 - [SS(s)/SS(s) + SS(n)]$$

where $SS(s) = \sum_{i=1}^{k} [X(i) - ES(i)]^2$ and

$$SS(n) = \sum_{i=1}^{k} [X(i) - EN(i)]^2.$$

$SS(s)$ = the sum of squared deviations for the southern regions,
$SS(n)$ = the sum of squared deviations for the northern regions,
$ES(i)$ = the 6-yr fitted average from the southern region,
$En(i)$ = the 6-yr fitted average from the northern region,
i = age,
$X(i)$ = the observed mean length at age (i),
k = the maximum age observed.

Thus, $Pr(s)$ is the likelihood of the cell being a southern cell. Arbitrary cut-off values of 0.75 and 0.25 were imposed to classify the southern and northern cells, respectively. Any value >0.25 and <0.75 defined an unknown cell.

New 6-yr average growth curves were fitted for each region by quarter and sex using only those estimates of mean length at age from cells that were classified as northern or southern (i.e., excluding all unknown cells). Partial F-tests showed ($P < 0.001$) that there are significant regional differences in growth between the "southern" (southeast shelf and slope) and the "northern" (Aleutian Basin and northwest slope) areas.

Using the new 6-yr average growth curves, the 1984 data were divided into cells, compared to Francis and Hollowed's (unpubl. data) growth curve, and were classified as northern, southern, or unknown, based on the index of similarity [$Pr(s)$] for both sexes combined:

$$Pr(s) = 1 - [SS(s)_{♀} + SS(s)_{♂}/SS(s)_{♀} + SS(s)_{♂} + SS(n)_{♀} + SS(n)_{♂}]$$

The classification of the 1984 data was examined to see whether the northern and southern cells fell into the same geographic areas as those which originally defined the growth types described by Lynde et al. (fn. 2) and the growth curves of Francis and Hollowed (i.e., the northwest slope and Aleutian Basin areas or the southeast shelf and slope areas).

Analysis of Fecundity

Collections of walleye pollock ovaries for fecundity analysis were subsampled by geographic area to provide at least four ovaries in each 5 cm length interval over the entire available length range. Ovaries were collected from walleye pollock in all areas except the northwest shelf, where observer coverage was inadequate. The oocytes were separated from the ovarian tissue by washing them through successively finer meshed sieves; and a volumetric subsampling method, similar to that described in Gunderson (1977), was used to estimate the total number of oocytes in each ovary. In all ovaries examined, there was a clear separation in the sizes of unyolked (uncounted) and yolked (counted) oocytes. The histological analysis (described below) indicated that ovaries showing this separation in egg size modes were at the stage of maturity suitable for fecundity counts. A minimum of five subsamples were counted for each ovary; if the coefficient of variation between subsample counts exceeded 10%, more counts were done, to a maximum of 10 counts. It was discovered that recounts of individual subsamples accounted for very little of the overall variation between counts, so these were not done on a regular basis.

The average coefficient of variation between subsample counts for each ovary was 5.20% (range, 0.87 to 10.30%). The number of oocytes was estimated for a total of 115 ovaries.

Fork length, ovary-free weight, and the mean of the subsample estimates of fecundity for each fish were used to derive three relationships for each area within the Bering Sea: length-fecundity, length-weight, and weight-fecundity. Nonlinear least-squares regression methods (Dixon 1983) were used to estimate parameters for each relationship. Unequal error variances were observed in the dependent variables of weight and fecundity. This was accounted for by the use of weighting factors in the nonlinear regression procedure. The weighting factor used was the inverse of the variance of the dependent variable.

Because comparison of linear regressions is the most direct method and because the linear and nonlinear regressions showed the same relative positions for each area, Newman-Keuls multiple range tests (Zar 1974) were done on the slopes and intercepts of the equations resulting from the linear regressions, to examine differences in the relationships by area. The regressions were fitted to a length range (38 to 60 cm) common to all areas before comparison.

Tests performed included an overall test for coincidental regression, Newman-Keuls multiple range tests on the slopes of the lines, and multiple range tests for equality of the intercepts of those relationships found to have equal slopes. The procedures outlined in Zar (1974) were followed for all of these tests. If the tests indicated that the relationship under examination did not differ significantly between two or more areas, the data from the areas were combined and a curve fitted to the new set of data using the nonlinear procedure.

Histological Analysis

The ovaries of walleye pollock collected for histological analysis were classified by area, following the same geographic scheme used for the length-at-age and fecundity analyses. The collection was subsampled to obtain ovaries in a complete range of development from each of the five geographic areas. Sections were removed from the central portion of the ovaries. Tanino et al. (1959) have shown that there is no difference in the size composition of oocytes throughout walleye pollock ovaries. All sections were 6 to 10 μm in thickness and were stained with Mayer's haemotoxylin and eosin. In all, 122 ovaries were examined histologically.

Oocytes were classified into 12 categories of development (Hinckley 1986). The overall maturity of each ovary was based on the most advanced oocytes present, and each ovary was assigned to one of 10 maturity classes (Hinckley 1986).

Egg-stage frequency counts, as determined from the histological slides, were used to examine the process of oocyte development. A transect grid was drawn on each slide, and oocyte counts for each stage of development were made at each intersection on the grid. Stage 8 (tertiary yolk) and

stage 9 (nuclear migration) oocytes were called stage 8; stage 11 (maturation) and stage 12 (ovulation) were called stage 11, owing to the difficulty in consistently differentiating these stages. Counts from all points on the grid were combined into a total egg-stage frequency for each ovary. Development of the maturing oocytes could be followed by comparing the egg-stage frequencies for each level of maturity.

Slides were also examined for evidence of ovarian rematuration. Rematuring ovaries were defined as those containing identifiable postovulatory follicles (the remnant of the egg membrane left after ovulation and release of the oocyte); thick ovarian walls; and resorbing, unspawned, fully yolked oocytes in ovaries that also contained vitellogenic oocytes.

RESULTS

Spatial and Temporal Distribution of Spawning

Observer information showed that walleye pollock spawning in the Bering Sea began in the Aleutian Basin in January. As the year progressed, spawning was observed further inward over the continental slope and shelf (Fig. 2A through 2H). Spawning occurred between January and March in the basin, between March and June over the southeastern Bering Sea slope and shelf, and between June and August over the northwest slope and shelf. Scattered spawning was noted in the northwestern areas as late as October.

Spawning walleye pollock were caught at depths ranging from 46 to 360 m, most commonly between 100 and 250 m. Temperatures at these depths ranged from −1.8° to 6.0°C ($\bar{x}$ = 2.34°C).

The monthly distribution of the commercial fishing fleet in the Bering Sea was examined to assess whether observer reports from the fleet represented the true distribution of spawning. If significant portions of the Bering Sea were not fished by the fleet, concentrations of spawning walleye pollock could have been missed. In January and February, coverage of the continental shelf was scattered and in May most fishing occurred in the southeast portion of the Bering Sea. Coverage of the Aleutian Basin was minimal after March because harvestable concentrations of spawning walleye pollock could not be found in the area after this time (R. Nelson[5]). Nevertheless, the fishing fleet distribution appears to have been sufficiently extensive to detect the majority of spawning walleye pollock, and the reports of spawning obtained from the fleet appear to reasonably represent the true spawning distribution for 1984.

Length-Age Characteristics of Walleye Pollock from Spawning Concentrations

The plots of mean length at age for walleye pollock males (Fig. 3) and females (Fig. 4) suggest that length at age was similar for both sexes in the Aleutian Basin and over the northwest slope. Lengths for the older ages were smaller in these areas than in the other three. Although the data were widely scattered, length at age was similar in the southeast shelf, southeast slope, and northwest shelf, and was larger in these areas than in the basin and the northwest slope.

Comparison of the length-at-age data from ½° by 1° cells with the growth curves generated by Francis and Hollowed showed that most of the cells assigned to the "northern" group were in the northern slope and buffer areas and in the Aleutian Basin (Fig. 5). Walleye pollock in these areas were characterized by a smaller mean length at age. Cells designated as "southern" were mostly from the southeast and northwest shelf areas and southeast buffer zone (Fig. 5) and contained walleye pollock with a larger mean length at age. The spawning concentrations of walleye pollock, therefore, show the same geographic distribution of the two growth types as seen by Lynde et al. (fn. 2) and Francis and Hollowed (unpubl. data).

Length-Fecundity Relationship

In all areas of the Bering Sea, the length-fecundity relationship for walleye pollock (Fig. 6) was found to be curvilinear ($F = aL^b$, Table 1), similar to that observed for walleye pollock from other regions. The overall test for coincidental regression indicated ($F = 5.51$, $P < 0.001$) that the length-fecundity relationships for the four areas were not identical.

Multiple range test results (Table 2) indicated that the northwest and southeast shelf and slope area regression slopes did not differ significantly.

[5]R. Nelson, Observer Program, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. 1984.

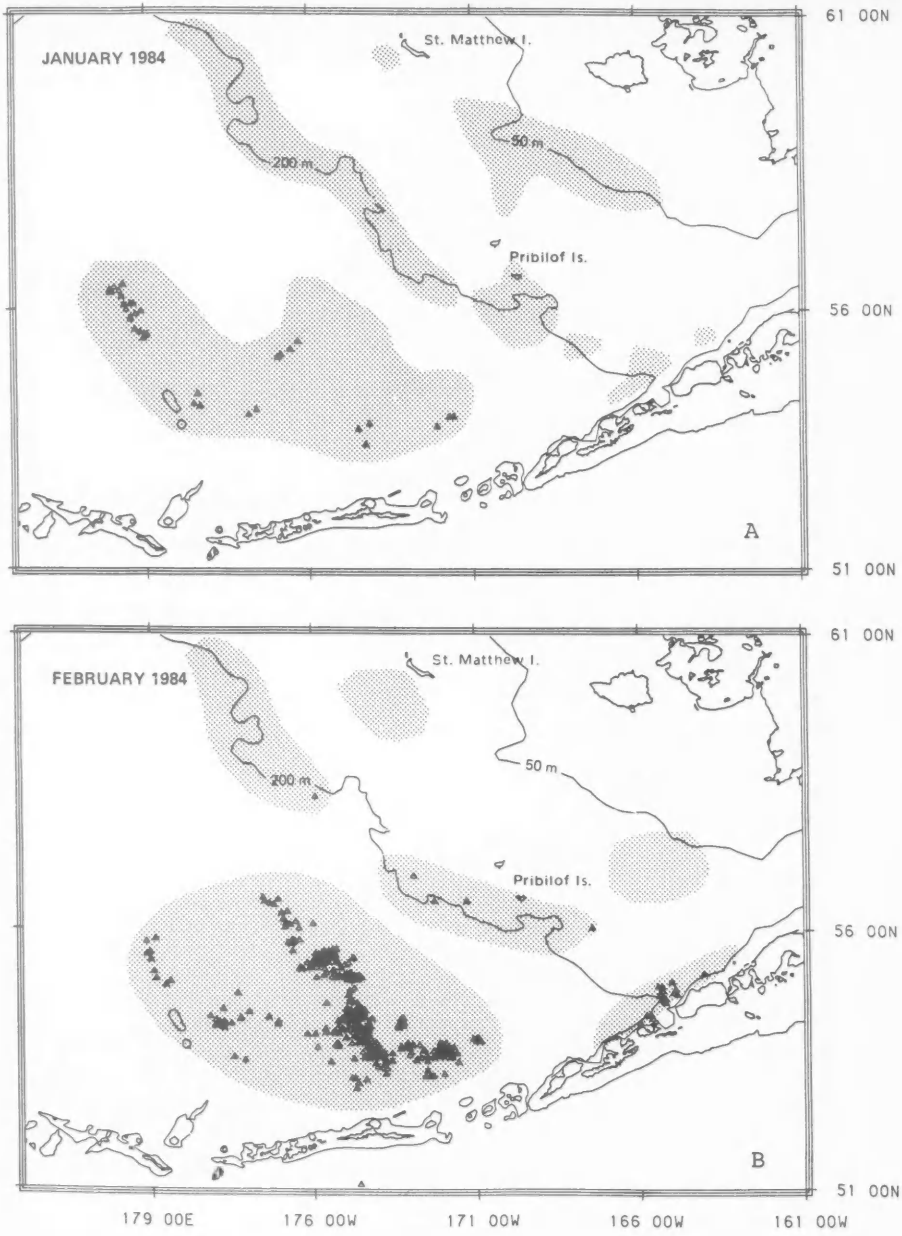


FIGURE 2.—Observed distribution of spawning walleye pollock in 1984, by month. Shaded areas indicate distribution of the

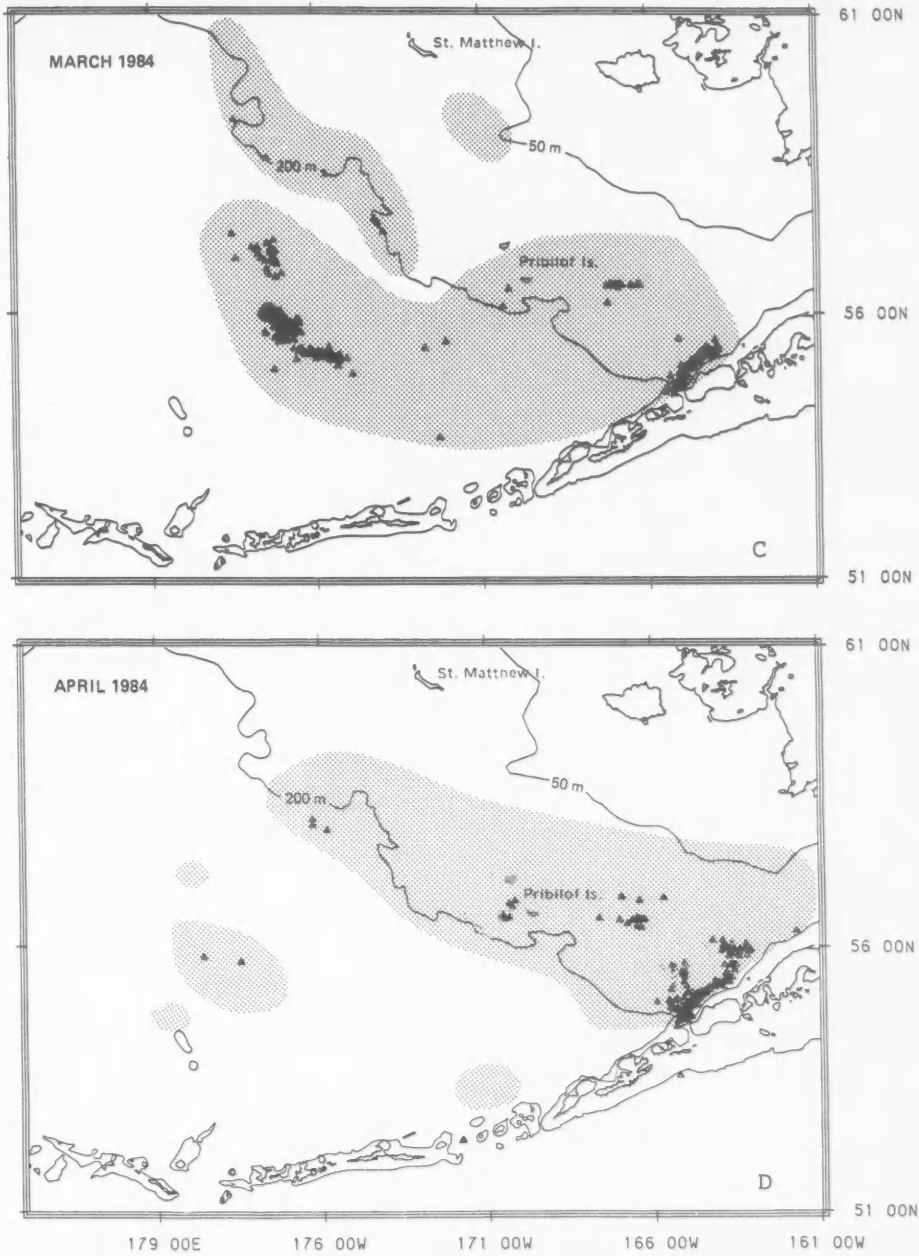


FIGURE 2.—*Continued*—foreign commercial fishing fleet. Triangles indicate hauls in which spawning walleye pollock were caught.

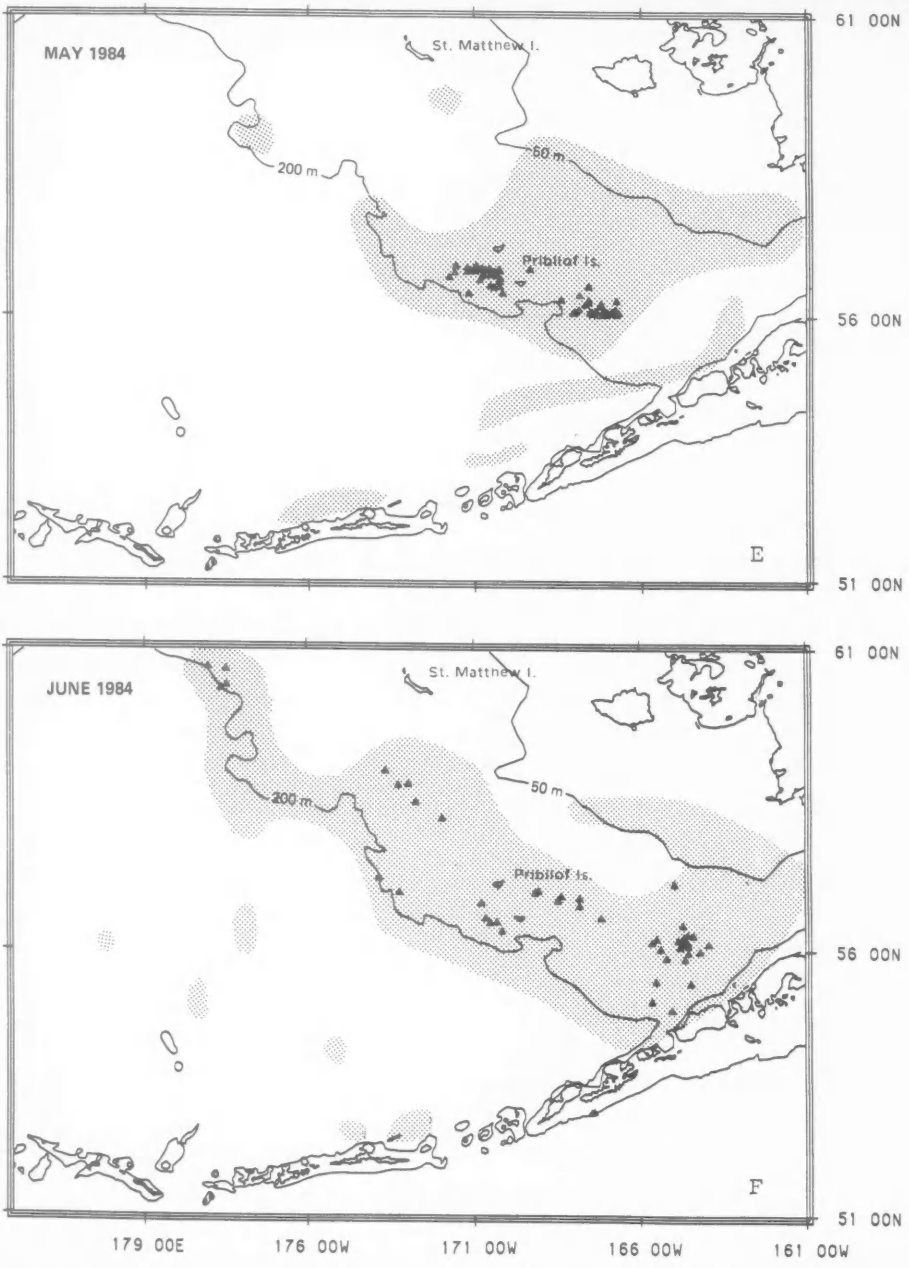
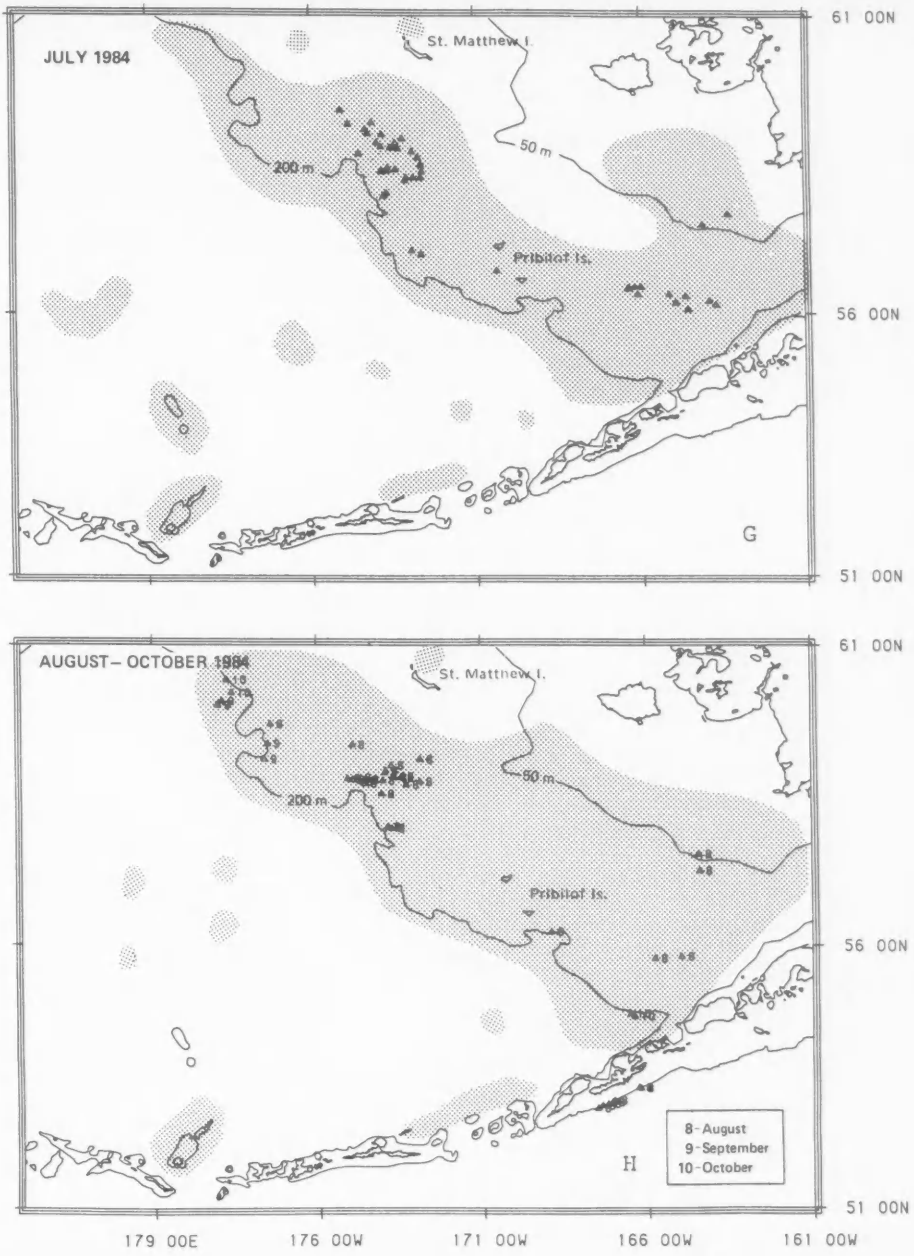


FIGURE 2.—*Continued.*



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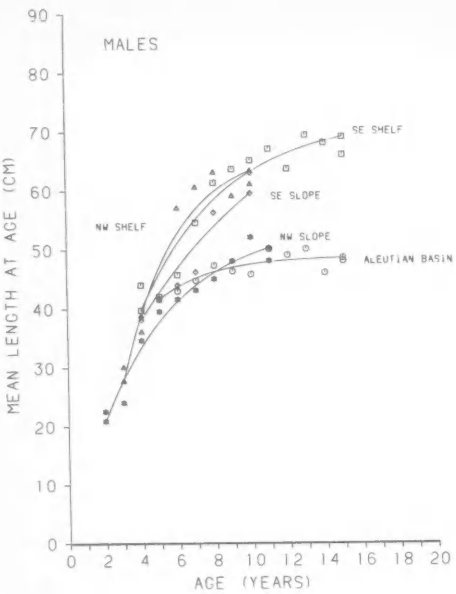

FIGURE 3.—Mean length at age for male walleye pollock from spawning concentrations in five areas of the Bering Sea. Squares indicate fish from the southeast shelf area; triangles, fish from the northwest shelf area; diamonds, fish from the southeast slope area; stars, fish from the northwest slope area; and circles, fish from the Aleutian Basin.

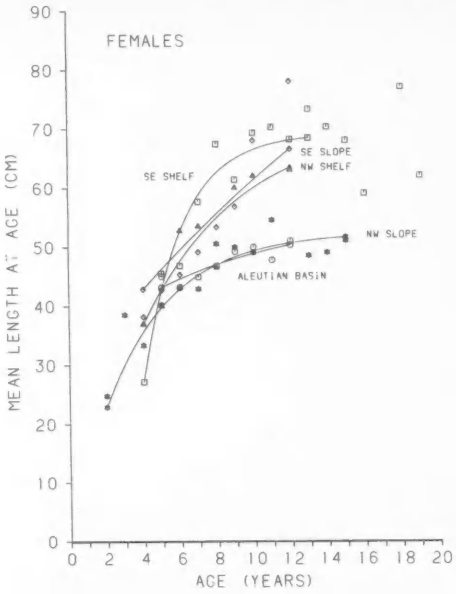

FIGURE 4.—Mean length at age for female walleye pollock from spawning concentrations in five areas of the Bering Sea. Squares indicate fish from the southeast shelf area; triangles, fish from the northwest shelf area; diamonds, fish from the southeast slope area; stars, fish from the northwest slope area; and circles, fish from the Aleutian Basin.

TABLE 1.—Length, weight (W), and fecundity (F) relationships for Bering Sea walleye pollock resulting from the nonlinear regression.

		Length-fecundity		Length-weight		Weight-fecundity	
Region	n	F	R^2	W	R^2	F	R^2
Southeast shelf	25	$0.1926L^{3.5439}$	0.865	$0.0120L^{2.8744}$	0.996	$91.7096W^{1.1423}$	0.877
Aleutian Basin	20	$469.2282L^{1.5575}$	0.769	$0.1257L^{2.2300}$	0.983	$9{,}119.3100W^{0.4570}$	0.737
Southeast slope	28	$4.6528L^{2.8066}$	0.944	$0.0041L^{3.1134}$	0.997	$906.4315W^{0.8534}$	0.935
Northwest slope	38	$0.0872L^{3.7869}$	0.995	$0.0001L^{3.4862}$	0.999	$118.6879W^{1.1439}$	0.995
Combined areas	91	$^{1}0.1719L^{3.6046}$	0.907	$^{2}0.0027L^{3.2743}$	0.996	$^{1}174.9222W^{1.0765}$	0.900

The multiple range test on the regression intercepts could not distinguish the intercepts of the three lines from the slope and shelf areas. The multiple range test on regression slopes also showed that the slopes of the regressions from the Aleutian Basin and from the southeast slope areas could not be distinguished; however, the intercepts of the regressions from these two areas differed significantly.

Based on these analyses, the length-fecundity relationships from all shelf and slope areas appeared to be similar, and the relationship in these areas was different from that seen in the Aleutian Basin. Fecundity increased almost linearly with length in Aleutian Basin walleye pollock; however, pollock larger than about 60 cm are not found in the basin (Okada 1977[6], 1983[7]; J.

[6]Okada, K. 1977. Preliminary report of an acoustic survey of the pollock stock in the Aleutian Basin and the adjacent waters in the summer of 1977. Document submitted to the annual meeting of the International North Pacific Fisheries Commission, September 1977. Fishery Agency of Japan.

[7]Okada, K. 1983. Biological characteristics and abundance of the pelagic pollock in the Aleutian Basin. Document

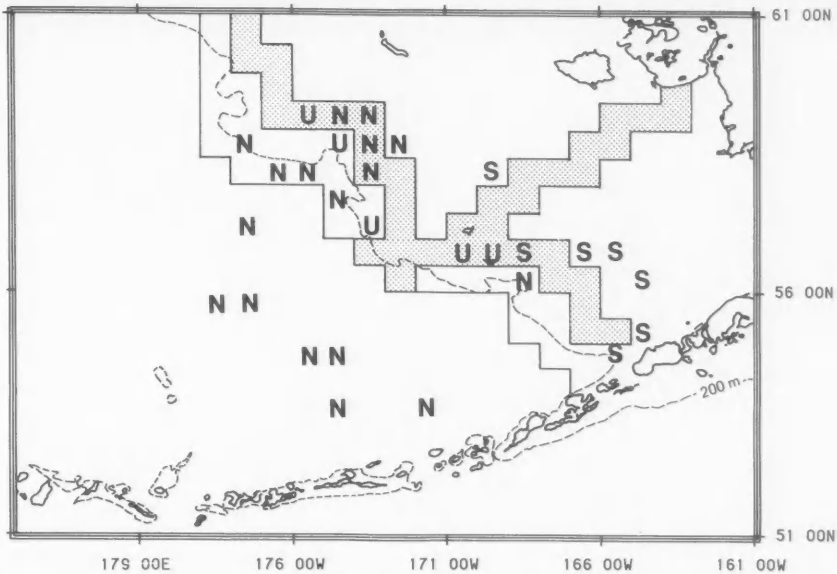

FIGURE 5.—Locations of cells containing walleye pollock from spawning concentrations with growth rates similar to "northern" (N), "southern" (S), or "unknown" (U) groups of Lynde et al. (text footnote 2).

Traynor[8]). The great increase in fecundity, seen in fish larger than 60 cm, resulted in the observed curvilinear relationships found in the other areas.

Length-Weight Relationship

The multiple range test results on the length-weight relationship for walleye pollock were inconclusive (Table 3). The hypothesis that the length-weight relationship was the same in all areas was rejected ($F = 3.4156$, $0.0025 < P < 0.005$), but the slopes of the regression lines did not differ significantly. A test of intercept equal-

submitted to the annual meeting of the International North Pacific Fisheries Commission, 1983. Far Seas Fisheries Research Laboratory, Japan.

[8]J. Traynor, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. 1984.

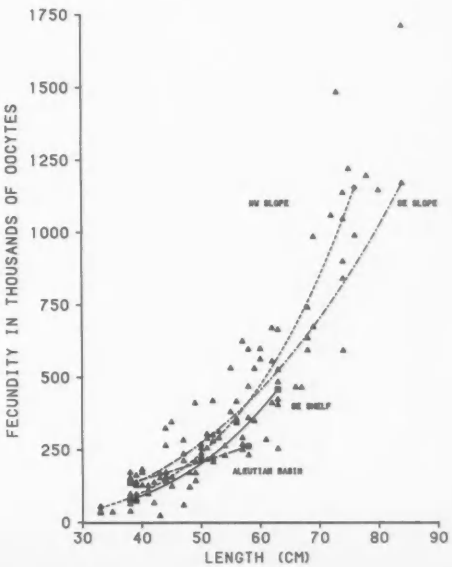

FIGURE 6.—Observed and predicted relationships between fecundity and length for walleye pollock from four areas within the Bering Sea. Triangles indicate the number of oocytes per sampled fish.

TABLE 2.—Newman-Keuls multiple range tests on the slopes and intercepts of the linearized length-fecundity regressions from four areas in the Bering Sea (following the notation of Zar 1974).

SLOPES

Ranks of slopes:	1	2	3	4
Ranked slopes:	1.6554	2.7661	4.0967	4.2659
Area:	Aleutian Basin	SE slope	SE shelf	NW slope

Comparison	Difference	SE	q	p	q(0.05,78,p)
4 vs. 1	2.6105	0.5320	4.9070	4	3.70
4 vs. 2	1.4998	0.5735	2.6152	3	3.37
4 vs. 3	Do not test				
3 vs. 1	2.4413	0.4926	4.9559	3	3.37
3 vs. 2	Do not test				
2 vs. 1	1.1107	0.5928	1.8737	2	2.81

INTERCEPTS

A.

Ranks of intercepts:	1	2	3
Ranked intercepts:	−4.211	−3.864	1.711
Area:	NW slope	SE shelf	SE slope

Comparison	q	p	q(0.05,60,p)
3 vs. 1	1.3870	3	3.40

B.

Ranks of intercepts:	1	2
Ranked intercepts:	1.711	5.784
Area:	SE slope	Aleutian Basin

Comparison	q	p	q(0.05,35,p)
2 vs. 1	3.6720	2	2.88

TABLE 3.—Newman-Keuls multiple range tests on the slopes and intercepts of the linearized length-weight regressions from four areas in the Bering Sea (following the notation of Zar 1974).

SLOPES

Ranks of slopes:	1	2	3	4
Ranked slopes:	2.7927	2.8883	3.1635	3.3161
Area:	Aleutian Basin	SE shelf	SE slope	NW slope

Comparison	Difference	SE	q	p	q(0.05,107,p)
4 vs. 1	0.5234	1.7581	0.2977	4	3.70

INTERCEPTS

Ranks of intercepts:	1	2	3	4
Ranked intercepts:	−6.3145	−5.6965	−4.5605	−4.1570
Area:	NW slope	SE slope	SE shelf	Aleutian Basin

Comparison	q	p	q(0.05,107,p)
4 vs. 1	6.2685	4	3.70
4 vs. 2	4.1848	3	3.37
4 vs. 3	1.4944	2	2.81
3 vs. 1	4.3880	3	3.37
3 vs. 2	2.5906	2	2.81
2 vs. 1	0.4340	2	2.81

ity showed a significant difference ($F = 3.608$, $0.01 < P < 0.025$); however, the multiple range test on intercepts was inconclusive and showed overlaps in the equality of intercepts by area. The curves in Figure 7 all appear similar. A nonlinear regression on the combined data from all areas explained a high percentage of the overall variation (99.63%) (Table 1). It seems reasonable to use one equation to describe the length-weight relationship for all areas combined.

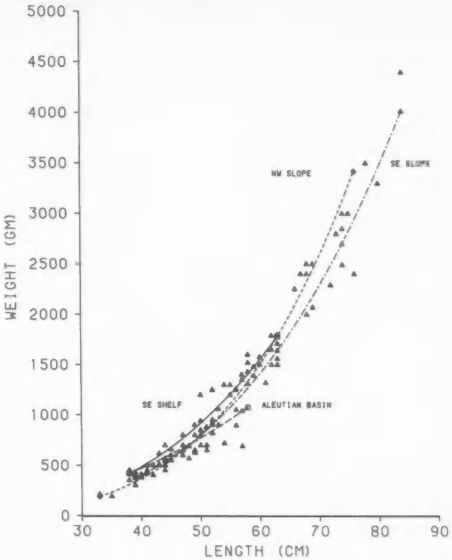

FIGURE 7.—Observed and predicted relationships between weight and length for walleye pollock from four areas within the Bering Sea. Triangles indicate the weight of the sampled fish.

Weight-Fecundity Relationship

The weight-fecundity relationship for walleye pollock in all areas was nearly linear (Fig. 8). The overall test for coincidental regressions indicated that the weight-fecundity relationship differed significantly between areas ($F = 7.6534$, $P < 0.001$). Comparison of the linearized equations showed that the regression slopes were similar in the northwest continental slope, the southeast continental shelf, and the southeast continental slope areas (Table 4). The multiple range test on the intercepts of the regressions from the two continental slope areas indicated that they were similar, but different from the regression intercept of the line from the southeast shelf area. The multiple range test on the regression slopes showed that the slope of the weight-fecundity regression for Aleutian Basin pollock was similar to that seen in the southeast continental slope area; however, a comparison of the intercepts did show a significant difference between these two areas.

As with the length-fecundity relationship, the weight-fecundity relationship appeared similar in the continental shelf and slope areas, and differed from the relationship seen in the Aleutian Basin. The weight-fecundity relationship for the Aleutian Basin showed the same trend that was seen for length-fecundity, i.e., a much more gradual increase in fecundity with weight than in other areas.

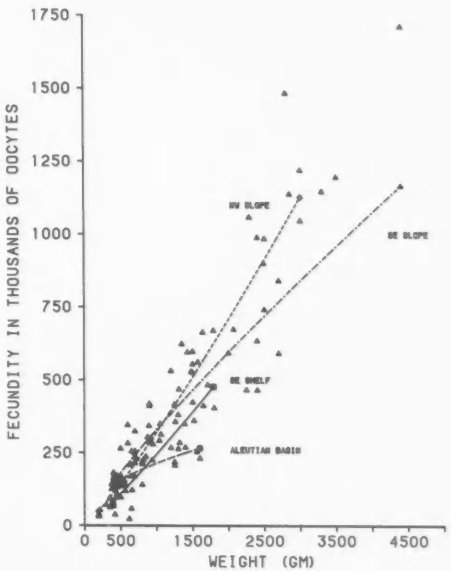

FIGURE 8.—Observed and predicted relationships between fecundity and weight for walleye pollock from four areas within the Bering Sea. Triangles indicate the number of oocytes per sampled fish.

Ovarian Maturation

Examination of the egg-stage frequencies indicates that the process of ovarian development in Bering Sea walleye pollock (Fig. 9A through 9M) is one of partial synchrony. A "reserve" fund (Foucher and Beamish 1980) of small, unyolked oocytes exists at all times in the ovary; this consists of oocytes at the early and late perinucleus stages. The reserve fund is represented by the single mode in Figure 9A. A portion of this group begins the process of yolk formation, advancing asynchronously to the fully yolked tertiary yolk stage (stage 8). This developing mode is visible in Figure 9B, C, and D. When vitellogenesis is complete, the mode of developing oocytes is com-

TABLE 4.—Newman-Keuls multiple range tests on the slopes and intercepts of the the notation

SLOPES

Ranks of slopes:	1	2	3	4
Ranked slopes:	0.5169	0.9577	1.2280	1.3978
Area:	Aleutian Basin	SE slope	NW slope	SE shelf

Comparison	Difference	SE	q	p	q (0.05,78,p)
4 vs. 1	0.8809	0.1555	5.6650	4	3.70
4 vs. 2	0.4401	0.1698	2.5919	3	3.37
4 vs. 3	Do not test				
3 vs. 1	0.7111	0.1574	4.5178	3	3.37
3 vs. 2	Do not test				
2 vs. 1	0.4408	0.1847	2.3866	2	2.81

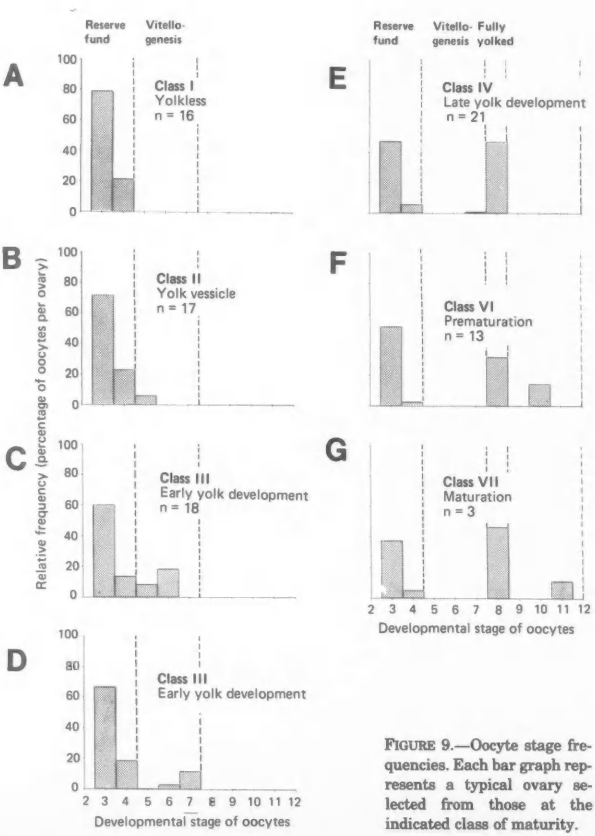

FIGURE 9.—Oocyte stage frequencies. Each bar graph represents a typical ovary selected from those at the indicated class of maturity.

inearized weight-fecundity regressions from four areas in the Bering Sea (following of Zar 1974).

INTERCEPTS

A.

Ranks of intercepts:	1	2	3
Ranked intercepts:	2.7420	4.2815	6.1588
Area:	SE shelf	NW slope	SE slope

Comparison	q	p	q(0.05,60,p)
3 vs. 1	6.4957	3	3.40
3 vs. 2	1.3520	2	2.83
2 vs. 1	5.4330	2	2.83

B.

Ranks of intercepts:	1	2
Ranked intercepts:	6.1588	8.7805
Area:	SE slope	Aleutian Basin

Comparison	q	p	q(0.05,35,p)
2 vs. 1	5.2249	2	2.88

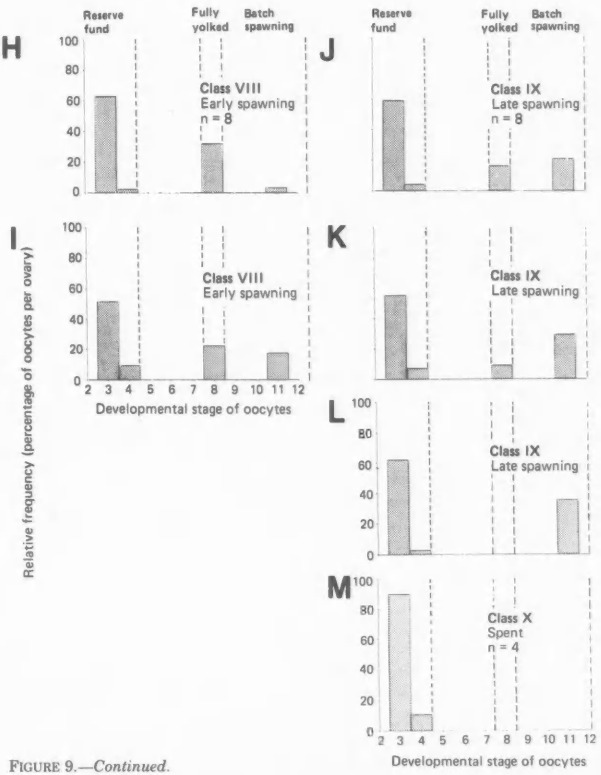

FIGURE 9.—*Continued.*

pletely separated from the remaining reserve fund (Fig. 9E). This appears to be the best stage to estimate fecundity, as no more eggs will be recruited into the developing mode, and spawning has not yet begun.

The final part of the maturation process appears to occur in a synchronized manner, with successive groups of fully yolked oocytes proceeding through the last stages (homogenization of yolk, hydration, ovulation, and release) in discrete batches. During the spawning period, the proportion of nonhydrated (stage 8) oocytes gradually decreases, and that of hydrated oocytes (stage 11) increases, until only hydrated oocytes remain. This progression is visible in Figure 9H through L. The spawning of matured oocytes in discrete groups appears to represent the "batch spawning" process in walleye pollock.

Spent ovaries contain oocytes in the early and late perinucleus stages (the reserve fund), postovulatory follicles, and, in some cases, yolked but unspawned oocytes undergoing resorption. Redeveloping ovaries, i.e., those containing signs of prior spawning and vitellogenic oocytes, were found in small numbers (9 out of 122 ovaries examined). Of the 18 ovaries examined for March, only one appeared to be developing new oocytes, possibly early enough for a second spawning that year. The rest of the redeveloping ovaries were collected from June to September from walleye pollock in the southeast shelf area. Redeveloped ovaries found in the summer with oocytes at the yolk vessicle stage may spawn in the autumn or during the next year (small numbers of walleye pollock have been observed in spawning condition throughout the year). Rematuring ovaries containing oocytes at the primary and secondary yolk stages were found only in August and September. More than one-half of these ovaries (5 out of 8) showed signs of resorption of the developing oocytes, and would probably not spawn again that year.

DISCUSSION

The results of this study appear to indicate that at least three separate spawning stocks of walleye pollock exist in the Bering Sea. One is located in the Aleutian Basin, a second over the northwest continental slope, and a third in the southeast shelf, southeast slope, and northwest shelf areas.

As noted by Ogawa (1956), geographical isolation or ecological separation of spawning concentrations may indicate population separation. Overall, the spawning season in the Bering Sea lasts about 8 months, and spawning within the different areas is separated by 500 to 1,000 km. Within the different areas, spawning lasts 2 to 3 months.

Dissimilarities in several population characteristics were observed between groups spawning in the different areas, supporting the concept of multiple stocks. Length at age differed by area, with larger length at age seen in walleye pollock spawning over the southeast shelf, southeast slope, and northwest shelf, and smaller length at age seen in walleye pollock spawning in the Aleutian Basin and over the northwest slope. These results were also found by Lynde et al. (fn. 2).

Fecundity relationships in all shelf and slope areas were similar, and differed from that seen in the Aleutian Basin. Aleutian Basin walleye pollock showed the lowest fecundity. Walleye pollock from the northwest and the southeast slope areas showed the highest fecundity. Fecundity estimates for walleye pollock in Shelikof Strait in 1982 (Miller et al. 1986[9]; $F = 1.2604L^{3.2169}$) and in British Columbia waters in 1979 (Thompson 1981; $F = 6.771L^{2.981}$) are higher than the Bering Sea estimates from this study. A general trend of declining fecundity exists towards the northern range of walleye pollock. Due to possible interannual variability in fecundity, caution should be taken in comparing studies done in different regions and years.

Further research is needed for walleye pollock, in the Bering Sea and elsewhere, to determine the proportion of annual fecundity actually realized, i.e., whether resorption of yolked oocytes during maturation and after spawning is significant. Preliminary histological analysis of walleye pollock ovaries from Shelikof Strait (Hinckley unpubl. data) suggests that resorption of yolked oocytes may not be significant.

Based on similarities in growth, Lynde et al. (fn. 2) proposed that mixing of walleye pollock stocks occurs between the Aleutian Basin and the northwest slope; however, the findings of this study indicate the mixing does not occur during the spawning season. Spawning over the basin and the northwest slope is separated by about 5 months and 500 km, yet there was no sign of

[9]Miller, B. S., D. R. Gunderson, D. Glass, D. B. Powell, and B. A. Megrey. 1986. Fecundity of walleye pollock (*Theragra chalcogramma*) from Shelikof Strait, Gulf of Alaska. Fish. Res. Inst. Rep. FRI-UW-8608. Univ. Washington, Seattle, WA 98195.

rematuration in walleye pollock ovaries collected from the northwest slope late in the season, which could have indicated that these fish spawned first in the basin and then later on the northwest slope. The difference in fecundity between these areas also supports the theory that spawners found in the northwest slope area form a separate group from those found in the Aleutian Basin. The similarities in growth found by Lynde et al. (fn. 2) may be a result of mixing occurring at other times of the year.

A reduced food supply may produce the smaller length at age and lower fecundity of Aleutian Basin walleye pollock. The reduced growth of walleye pollock in the basin is probably due to the lack of fish, particularly juvenile walleye pollock, in the diet (Okada fn. 7; Traynor and Nelson 1985; Dwyer et al. in press). Dwyer (1984) also found that the mean weight of stomach contents of basin-caught fish was low compared with that of fish caught over the shelf and slope. Reduced food supplies have been shown to lower fecundity in several species (Scott 1962; Hester 1964; Bagenal 1969; Leggett and Power 1969; Wootton 1973, 1977; Hislop et al. 1978).

Histological examination of walleye pollock ovaries further supports the theory that spawning concentrations found in widely separated areas do not mix extensively. Walleye pollock spawning in the Bering Sea can be classified as partially synchronous, with one discrete group of oocytes brought to maturation and then spawned in successive batches. This is similar to the process described for walleye pollock from Japan (Sakurai 1977). The maturation of a second group of oocytes from vitellogenesis to spawning within 1 year does not appear to be common. Maximum walleye pollock fecundity is therefore annually determinate, and the duration of an individual female's spawning period is limited by the duration of the batch spawning process. If an individual does batch spawn a group of matured oocytes over 1 month, as Sakurai's (1982) laboratory studies suggest, it seems unlikely that it would migrate any great distance over this time while actively spawning.

To infer stock separation from the results of this study (i.e., that fish return to the same discrete areas each year to spawn) requires assuming that the timing and distribution of spawning, the dynamics of ovarian maturation, and the differences in growth and fecundity remain relatively constant from year to year. The timing and location of spawning have been similar from 1982 to 1986 (Hinckley unpubl. data; R. Nelson fn. 5). The process of maturation is basically the same for walleye pollock found in the Bering Sea, in the Gulf of Alaska (Miller et al. fn. 9), and in Japanese waters (Sakurai 1977, 1982). Differences in mean length at age represent cumulative differences in growth over the life of a fish, and systematic variation by area such as that seen in this study probably reflects separation over a period of years. The study by Lynde et al. (fn. 2) documented the same differences in growth by area over a period of 8 years as was seen in this study for 1984. It is not known at what point annual fecundity is determined in walleye pollock, but as egg production is influenced by food supply in many species, and as walleye pollock feed mostly during the spring and summer and less during the winter (Dwyer et al. 1986) and the spawning season, yearly fecundity may be determined about 1 year before spawning. The results of this study suggest that the assumption of stock separation over a period of years is reasonable.

This study has outlined the timing and distribution of walleye pollock spawning in the Bering Sea for 1984, and postulates the existence of at least three separate spawning stocks. Further research is needed on the biological and oceanographic conditions occurring in the different spawning areas in order to understand the reasons for the apparent separation of stocks, and to clarify differences in recruitment and production by these stocks.

ACKNOWLEDGMENTS

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DISTRIBUTION, FEEDING, AND GROWTH OF LARVAL WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, FROM SHELIKOF STRAIT, GULF OF ALASKA

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ABSTRACT

Walleye pollock in the Gulf of Alaska have recently been found to form an intense spawning aggregation in late winter in Shelikof Strait. This produces a dense patch of planktonic eggs in early April, and later in spring a patch of larvae that can be followed as it drifts to the southwest. The density of larvae observed in 1981 indicated that density-dependent effects on feeding may be important for larval survival. In May 1983 we conducted a field study to investigate spatial and vertical distribution, feeding, and growth of larvae from this spawning. During this study we found, in an area of maximum concentration (~1 larva m^{-3}) located by an initial survey, larvae averaged 11.1 mm SL, and were similar in size to those found elsewhere. The larvae in 1983 were larger, and less abundant than at the same time in 1981. Larval growth was estimated from the number of otolith daily growth increments at size of larva and was similar in the area of maximum concentration and in other areas. Larvae were concentrated vertically between about 15 and 50 m and showed a crepuscular pattern of increased density at 14-28 m during twilight. Neither the vertical nor horizontal patterns of larval occurrences seemed closely associated with particular values of temperature or salinity. Most larvae were found in a temperature range of 7.0°-5.5°C and a salinity range of 31.5-32.2‰. Guts of larvae collected during darkness contained less food than those from daytime. Copepod nauplii were largely replaced by *Pseudocalanus* spp. copepodids in the diet of larvae larger than 14 mm. At the densities of walleye pollock larvae observed in this study, it appears that zooplankton production in the area did not impact larval growth, even in the area of maximum density.

A large spawning concentration of walleye pollock, *Theragra chalcogramma*, was discovered in 1980 in Shelikof Strait, and subsequently a 220,000 metric ton/year fishery developed. Shelikof Strait, a 50 by 200 km body of water in the northern Gulf of Alaska, between the Kodiak Archipelago and the Alaska Peninsula, is apparently the major spawning center for Gulf of Alaska walleye pollock. Ichthyoplankton surveys in 1981 and 1982 showed that spawning occurs primarily in a restricted area within Shelikof Strait and over a short period of time, producing a dense patch of eggs. Thereafter, larvae drift southwest with prevailing currents (Fig. 1). The densities of walleye pollock eggs and early larvae found in Shelikof Strait in 1981 exceeded 50 m^{-3} (Dunn et al. 1984[5]), far greater than their densities in the Bering Sea (Kim and Kendall 1983[6]) or Funka Bay, Japan (Hayashi et al. 1968); moreover, these densities significantly exceed those reported for larvae of any other fish (Hempel 1979).

Energetic requirements of larvae in high densities may exceed production of food and possibly lead to density-dependent effects on larval growth and survival (Jones 1973). At larval densities frequently found (ca. 1 m^{-3}), density-dependent effects are not considered important (McGowen and Miller 1980; Cushing 1983). Laboratory studies, however, have demonstrated effects of stocking

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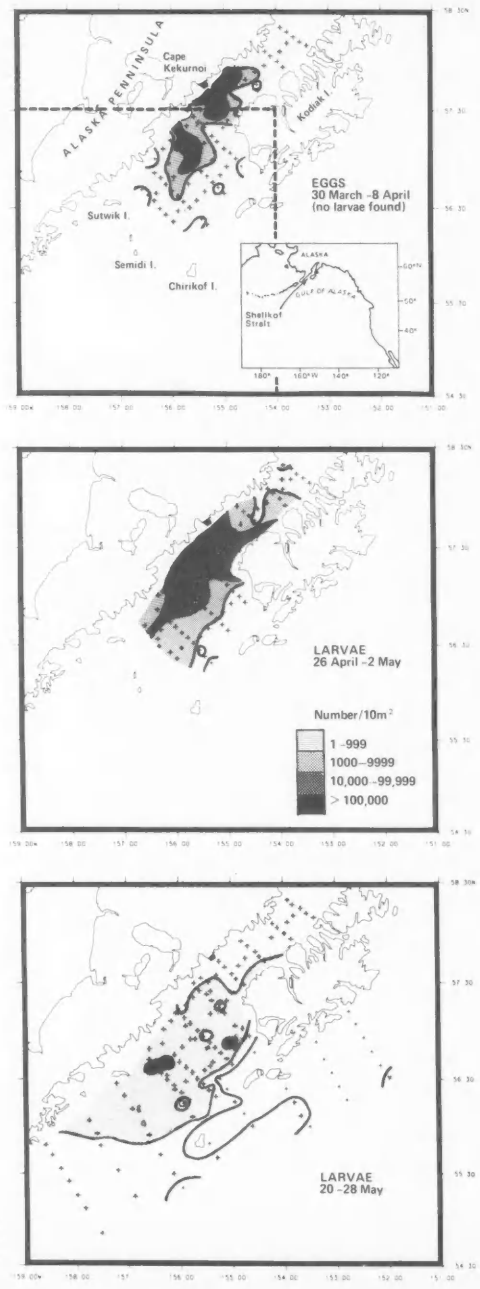

FIGURE 1.—Distribution and abundance of walleye pollock eggs and larvae, spring 1981. Based on Bates and Clark (text fn. 9). Cape Kekurnoi is blackened as a point of reference. Area shown in Figures 2 and 6 is outlined is upper panel.

density upon growth (O'Connell and Raymond 1970; Houde 1975), and recent studies on patches of larvae co-occurring with prey suggest that enhanced growth may be observed at high prey concentrations in the field (Govoni et al. 1985). Search volumes of 5 mm larvae morphologically similar to walleye pollock are about 10 L per day (Laurence 1982); thus with densities of 1 larva in 25 L found in Shelikof Strait in 1981, it is possible that density-dependence is important in larval feeding rate and growth.

Walleye pollock is widely distributed in the subarctic North Pacific. Larval feeding habit studies have been conducted in Uchiura Bay, Hokkaido, Japan (Kamba 1977) and in the southeastern Bering Sea (Clarke 1978) where the principal prey has been found to be copepod nauplii with *Pseudocalanus* spp. becoming increasingly important as the larvae grow. Larval growth in the same areas has been studied by Hayashi et al. (1968) and Nishimura and Yamada (1984) for Hokkaido and by Walline (1985) and Clarke (1984) for the Bering Sea. Growth rates in field collections and laboratory rearing studies have been shown to be quite variable, from about 0.16 to 0.37 mm d^{-1} (Bailey and Stehr 1986).

We conducted a field study to investigate the ecology of larval walleye pollock in Shelikof Strait in May 1983 by locating and sampling the densest patch of larvae. Here we report on growth, feeding habits, and depth distribution of larval walleye pollock we collected.

METHODS AND MATERIALS

Field Collections

An ichthyoplankton survey of 63 stations on a 15 nmi (27.8 km) grid southwest of Kodiak Island, AK, was conducted aboard the NOAA ship *Chapman* from 21 to 28 May 1983 (Fig. 2). At each station a MARMAP double oblique bongo tow (Posgay and Marak 1980) was made from the surface to 200 m (as water depths permitted) with a 60 cm bongo net equipped with 505 μm mesh nets. Flowmeters were mounted in the net mouths and a bathykymograph was used to determine the maximum tow depth and to evaluate the tow profile. A neuston net (Sameoto and Jaroszynski 1969) with 505 μm mesh was also towed for 10 minutes at each station. The neuston net sample and one of the bongo net samples at each station were preserved in 5% sodium borate buffered formalin in seawater. Most walleye pollock larvae from the other bongo net were rough sorted at sea and were immediately preserved in buffered 90% ethanol for otolith examination.

The results of the sorting of larvae at sea were used to choose a location of high larval density for the diel feeding/distribution study (Fig. 2). Another oblique tow, after this survey, confirmed the presence of high concentrations of larvae. Several preliminary tows with four 20 cm bongo nets on the towing wire fixed at 10 m depth intervals (between 5 and 91 m) were made to find depths of maximum larval concentrations. A tow was then taken every 4 hours for 48 hours during 28-30 May 1983 with 20 cm bongo nets equipped with 253 μm mesh nets on one side and 333 μm mesh nets on the other. Four nets were fished simultaneously for 10 minutes at a ship speed of approximately 100 cm/second. The nets were placed on the wire to fish at four depths within the region of larval abundance (nominally 20, 30, 40, and 50 m). Flowmeters were mounted in the mouths of the nets, and a bathykymograph was deployed with the deepest net to record actual tow depths. During setting and retrieving, the ship maintained reduced speed to minimize fishing outside the chosen depth strata. Thus, although no closing devices were used, nearly all of the water passing into the nets was at the chosen depth (Kendall and Naplin 1981). Tows were made at 1030, 1430, 1830, 2330, 0230, and 0630 local time (sunrise was at 0455 and sunset 2138 h). During the sampling of the stations at 1430 and 0230 on both days, a 1 m^2 mechanical Tucker trawl with 505 μm mesh was fished for 10 minutes at 35 m to investigate escapement from the 20 cm bongo nets. Also during the second 24-h period a 60 cm bongo net with 505 μm mesh was fished about 2 m below the deepest 20 cm bongo net to stabilize the wire and allow further catch comparisons.

Expendable bathythermograph (XBT) casts were done at each survey grid station and at the 1430 and 0230 vertical distribution study stations. Conductivity-temperature-depth (CTD) casts (Ocean Data Equipment Corporation[7] Model 302) were made at 15 of the survey grid stations selected to provide three sections across the major southwesterly setting flow field in the area (Fig. 2).

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

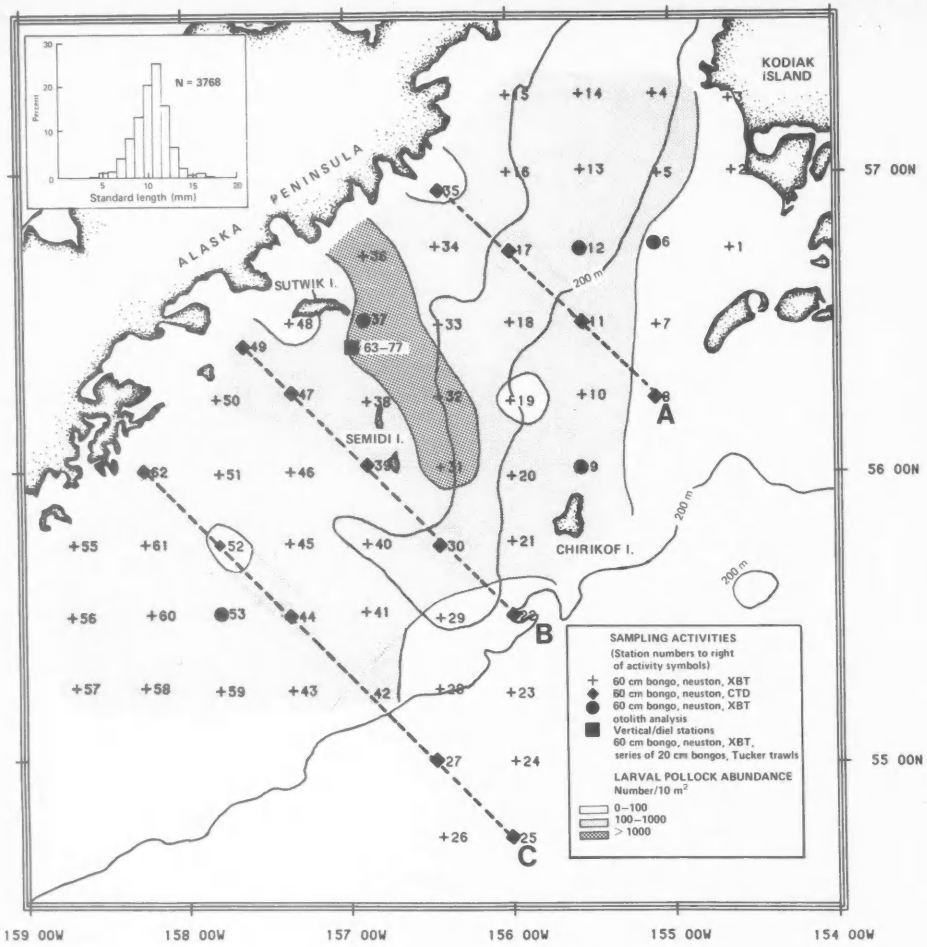

FIGURE 2.—Distribution, abundance (numbers per 10 m^2) and lengths of walleye pollock larvae from 60 cm MARMAP bongo tows superimposed on sampling pattern used in the northern Gulf of Alaska, May 1983. Hydrographic sections are labelled A, B, C (see Figure 4).

Laboratory Procedures

Fish eggs and larvae were identified to the lowest taxon possible at the Polish Plankton Sorting Center in Szczecin, Poland. Fish larvae were measured to the nearest 0.1 mm standard length (SL); when more than 50 larvae of a taxon occurred in a sample, a random subsample of 50 was selected for measurement. Identifications were verified at the Northwest and Alaska Fisheries Center. For distributional analysis of fish eggs and larvae from the survey, numbers per tow for each taxon were converted to numbers under 10 m^2 of water surface using volumes of water filtered and maximum tow depth (see Smith and Richardson 1977). To compare relative abundances of various taxa, an estimate of the total number of eggs or larvae of each taxon present in the entire survey area was derived by summing the catches at each station and multiplying by the

area of sea surface represented by that station (the Sette-Ahlstrom method, see Smith and Richardson 1977). This estimate was thought to make best use of all the available data.

A chi-square test analyzed differences in the numbers of walleye pollock larvae caught as a function of time of day and depth at the diel station. For this test, numbers of larvae in the two sides of the 20 cm bongo nets were combined. Also, catches at the same time and depth but on different days were combined when complete depth series were collected. Four out of six times two complete depth series were collected; at two times only one complete depth series was collected.

Zooplankton were sorted, identified, and enumerated from subsamples of collections made with the 253 μm mesh net. The subsample was chosen such that at least 500 organisms were sorted from each sample.

For larval feeding analysis, 20 walleye pollock larvae (or the total sample when <20 were caught) were selected to represent the size range in the total sample from each of the 333 μm mesh, 20 cm bongo net samples. The guts were dissected from the larvae, and all food items in the foregut, midgut, and hindgut were teased out, identified, and counted.

Lengths and greatest widths were measured for all food items in the larvae collected at 0630, 29 May. Lengths used were carapace length for copepod nauplii, metasome length for copepodids, and total length for all other prey. These measurements were used to estimate volumes of prey organisms, which were applied to the rest of the samples. Mensuration formulae were used to calculate the volume of copepod eggs, copepod nauplii, copepodids of *Pseudocalanus* spp., *Acartia* spp., and *Oithona* spp. (Nishiyama and Hirano 1983; Table 1). *Pseudocalanus* spp. mensuration formulae were used to estimate the volumes of unidentified copepodids. The volumes of other food items were not estimated since their low abundance did not allow adequate measurement of body proportions.

Samples used for age and growth analysis were selected from one station within the area of highest larval density (Station 37, Fig. 2), and from four stations located outside of this dense patch. Standard lengths of larvae from as broad a size range as possible within each sample were measured to the nearest 0.1 mm using an ocular micrometer. Both sagittal otoliths were removed and cleaned using a pair of fine needles under a dissecting microscope fitted with polarizing filters. Whole otoliths were affixed to microscope slides with clear histological mounting medium and increments read in the sagittal plane under a compound microscope with transmitted light at 1000× magnification. Most of the otoliths had a distinct distal-proximal curvature and readability was enhanced when the otolith was mounted with the concave side up.

Increments were identified as a pair of adjacent light and dark bands, formed concentrically around the focus. A prominent dark band surrounding the focus was observed on each otolith (Fig. 3). Since mean otolith diameter at this band (16.0 ± 0.13 μm SE) was similar to the diameter of otoliths from 1-day-old, laboratory-reared larval pollock (18.97 ± 0.37 μm, Nishimura and Yamada 1984; 16-20 μm, Walline 1983; 15.3 ± 1.2

TABLE 1.—Mensuration formulae (Nishiyama and Hirano 1983),[1] length to width ratios, metasome to whole body ratios, metasomal lengths, mean lengths, and mean diameters used to calculate volumes of copepodids, copepod nauplii, and copepod eggs in guts of larval walleye pollock in Shelikof Strait.

Species	K Length:width (this study)	m Metasome:whole body (Nishiyama and Hirano 1983)	Lm Metasomal length (this study)
Pseudocalanus spp.	2.239	0.97	0.870
Oithona spp.	1.824	0.93	0.189
Acartia spp.	3.213	0.95	0.916
Unidentified copepodids	2.539	0.97	0.870

[1]Mensuration formulae (Nishiyama and Hirano 1983):
Volume of copepodids = $[Lm/6 \cdot (Lm/K)^2 \cdot \pi]/m$.
Volume of copepod nauplii = $\left(\frac{\pi}{24} \text{ carapace length}^3\right)$;
mean carapace length = 0.187.
Volume of copepod eggs = $\left(\frac{\pi}{6} \text{ egg diameter}^3\right)$;
mean egg diameter = 0.110.

μm, Bailey and Stehr[8]), this band was presumed to be the hatching check and was counted as the first increment. Nishimura and Yamada (1984) found that increments were formed daily, beginning with the day of hatching, on the otoliths of laboratory-reared larval pollock. Similar observations have been made on larval walleye pollock otoliths viewed with both light and scanning electron microscopy by Bailey and Stehr (fn. 8). Increments were, therefore, considered to be deposited daily and increment counts were equated with the age of the fish in days after hatching.

The mean of two independent increment counts was used in growth rate analysis. Age-at-length data from each station were fitted separately with simple linear regressions. Analysis of covariance was used to compare growth rates and Dunnett's test of multiple comparisons identified significantly different rates (Zar 1974).

[8]K. Bailey and C. Stehr, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way, N.E., Seattle, WA 98115, pers. commun. 7 February 1985.

RESULTS

Hydrographic Observations

Temperature in the survey area varied from just above 7°C at the surface at some stations to slightly <5°C in deeper shelf water (Fig. 4). Temperature gradually decreased with depth, and temperatures in the upper 50 m (where most of the walleye pollock larvae were found) were generally between 7.0° and 5.5°C. At the diel-vertical distribution station, temperatures were similar to those found throughout the area, although the temperature gradient was more uniform than elsewhere. In the upper 60 m at this station, tem-

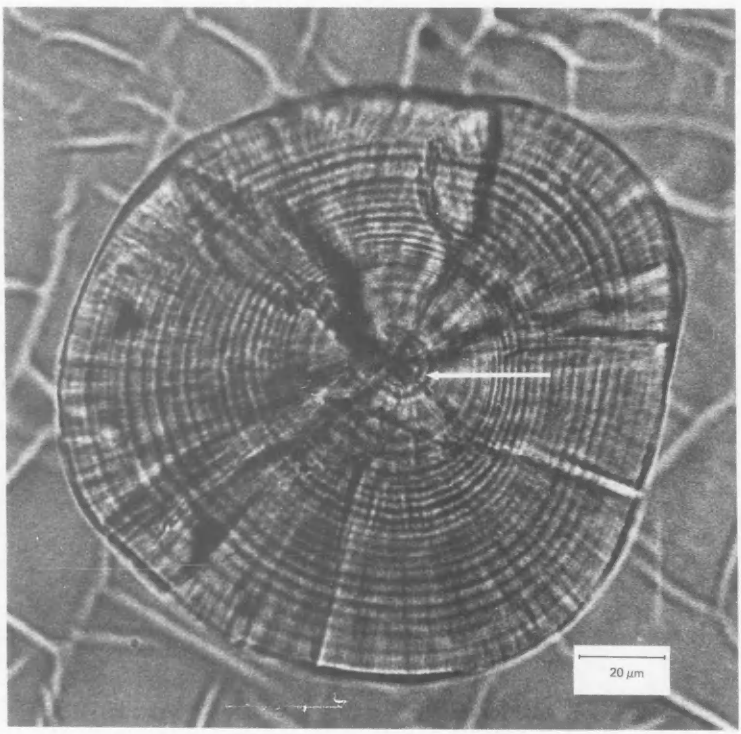

FIGURE 3.—Otolith from a 11.57 mm SL walleye pollock larva showing 27 daily growth increments. The arrow near the focus indicates the first increment. Scale bar indicates 20 μm.

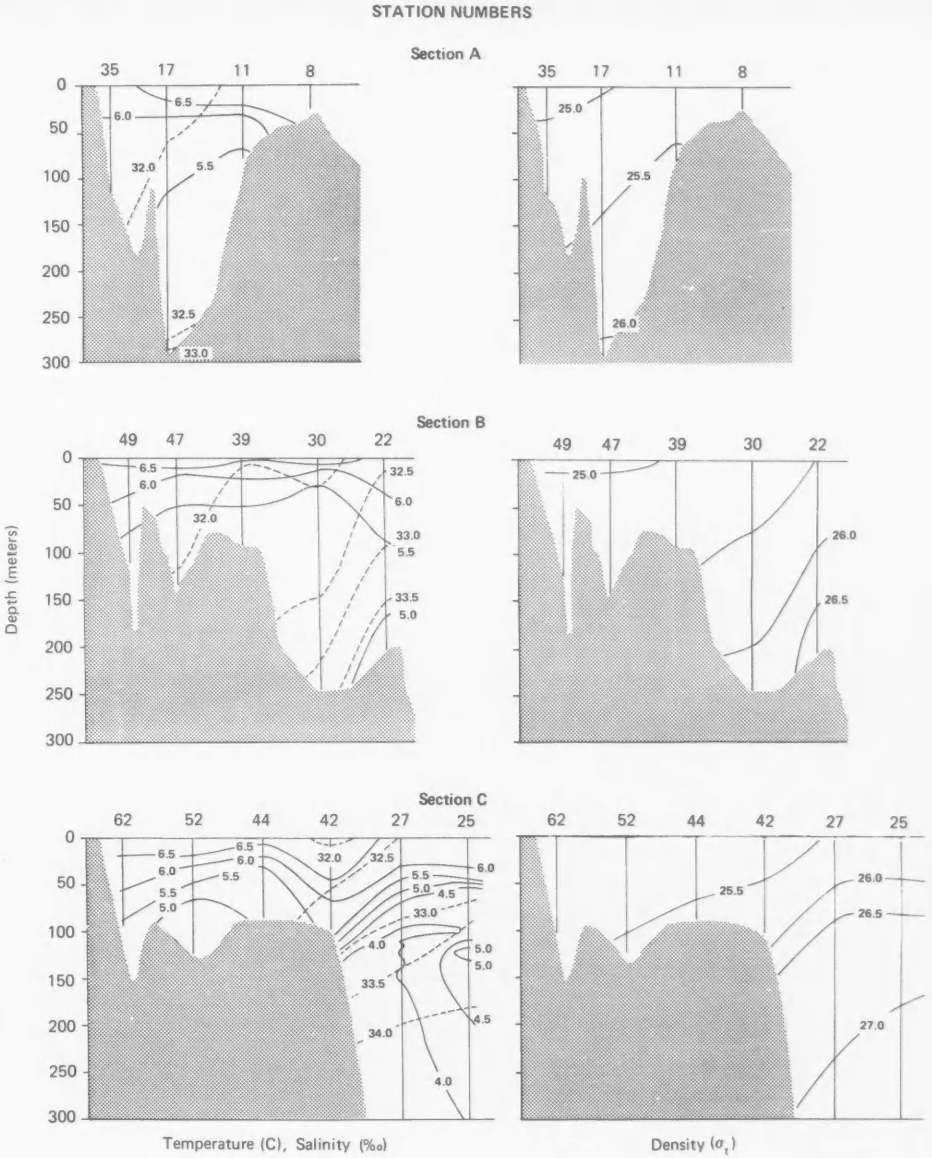

FIGURE 4.—Temperature (solid contours), salinity (broken contours), and density observed in three sections across the sampling area, May 1983. Station and section locations are shown in Figure 2.

perature steadily decreased from 6.9°C to 6.0°C, and at the bottom (120 m) the temperature dropped to 5.5°C. Among the four XBT casts (taken at 12-h intervals), the temperature at a given depth varied as much as 0.5°C: an isotherm depth varied vertically by as much as 50 m.

Salinity varied from 31.5 to >33.5‰ in the survey area. Lowest salinities were found at the surface toward the Alaska Peninsula, and high salinities were found offshore in deeper waters. Isohalines generally sloped from offshore to inshore. This slope was most pronounced at Section A, the one closest to Shelikof Strait. Most larvae were in water between 31.5 and 32.2‰. The salinity profile at the CTD station closest to the diel station showed a slight and steady increase in salinity with depth starting from a surface value of 31.8‰ and ending with a bottom (142 m) value of 32.1‰.

Density sections (σ_t) show the same sloping pattern as the salinity sections but are even more pronounced (Fig. 4). Values ranged from <25.0 at the surface near the Alaska Peninsula to >26.4 in deeper waters near the edge of the continental shelf. No sharp pycnocline was observed but rather a gradual increase in density with depth and distance from the Alaska Peninsula. Most walleye pollock larvae were in water with densities between 25.0 and 25.4 σ_t. The density profile observed near the diel station closely paralleled the salinity profile, with a gradual increase with depth from $\sigma_t = 24.9$ at the surface to $\sigma_t = 25.4$ at the bottom (142 m).

Relative Abundance of Eggs and Larvae

Neuston tows and bongo tows captured eggs of 13 and 14 taxa, respectively (Fig. 5). Rank orders of abundance, based on estimated total numbers of fish eggs in the neuston catches showed *Microstomus pacificus* (Dover sole) to be in greatest abundance, followed by *Glyptocephalus zachirus* (rex sole) and *Theragra chalcogramma*. In bongo catches, unidentified pleuronectid (righteye flounders) eggs were most abundant, followed by those of *M. pacificus, G. zachirus,* and *T. chalcogramma.*

Larvae of 29 and 42 taxa were identified in neuston and bongo catches. Rank order of abundance of fish larvae in neuston tows, based on estimated total numbers, showed *Ammodytes hexapterus* (Pacific sand lance) to be most abundant followed by *Hexagrammos decagrammus* (kelp greenling), *Lyconectes aleutensis* (dwarf wrymouth), *Bathymaster* spp. (ronquils), and *T. chalcogramma.* In bongo catches *T. chalcogramma* larvae were most abundant followed by those of *Bathymaster* spp., *A. hexapterus, Hippoglossoides elassodon* (flathead sole), and unidentified gadids (codfishes).

Distribution and Abundance of Walleye Pollock Eggs and Larvae

Eggs of walleye pollock were taken in 26% of the bongo tows and in 27% of the neuston tows but in low abundance. Only 262 eggs were collected. Some early stage eggs were collected, indicating recent spawning, but older eggs were also present. Eggs were found mainly in water over the deeper part of Shelikof Strait, with decreasing abundance to the southwest (Fig. 6).

Larvae of walleye pollock were found in 89% of the bongo catches and 24% of the neuston catches. The center of larval concentration was near the middle of the survey pattern (Fig. 2). Mean standard length of the larvae throughout the survey was 10.63 mm (range 3.8-21.3 mm, SD = 1.81 mm), with no differences in mean length by area. At each of five stations near Sutwik Island and the Semidi Islands, more than 1,000 larvae/10 m^2 were encountered. At 44 of the 64 stations, more than 100 larvae/10 m^2 were found. A total of over 10^{12} larvae was estimated to be present in the survey area.

Vertical Distribution of Walleye Pollock Larvae

In preliminary tows with the 20 cm bongo nets most larvae were caught above 60 m. During the vertical distribution study actual depths of sampling based on bathykymograph records covered the ranges of 14-20, 21-28, 28-38, and 39-47 m (Table 2).

The mean length of the larvae during our diel vertical distribution study was 11.1 mm SL. The range of mean lengths among the individual samples was 10.0-12.2 mm SL, and the range of standard deviations was 0.8-2.3 among hauls with more than 10 larvae. No patterns of size of larvae with depth or time of day were seen by visual inspection of the data, and since the range of mean lengths was so narrow, and the confidence intervals overlapped, no further analysis was performed.

There were no diel differences in catch rates

FIGURE 5.—Rank order abundance, as log of total numbers in the survey area, of fish eggs and larvae in neuston and bongo tows during the survey, May 1983.

TABLE 2.—Chi-square test of numbers of walleye pollock larvae with time and depth from the vertical distribution study, May 1983.

	Time											
	1840-1920		2235		0320-0238		0629-0635		1047		1432-1515	
	No. samples											
Depth	16		8		16		16		8		16	
(m)	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
14-19	76	(94)	98	(78)	133	(159)	100	(59)	61	(68)	37	(47)
21-28	76	(122)	138	(101)	202	(207)	68	(76)	108	(89)	65	(62)
28-38	110	(95)	11	(79)	201	(161)	46	(59)	87	(69)	56	(48)
39-47	136	(87)	83	(72)	140	(148)	35	(55)	33	(63)	43	(44)
Total	398		330		676		249		289		201	
χ^2	52.19		78.89		14.73		39.46		23.77		3.63	

Total $\chi^2 = 212.69$ (15 df, $P < 0.005$)

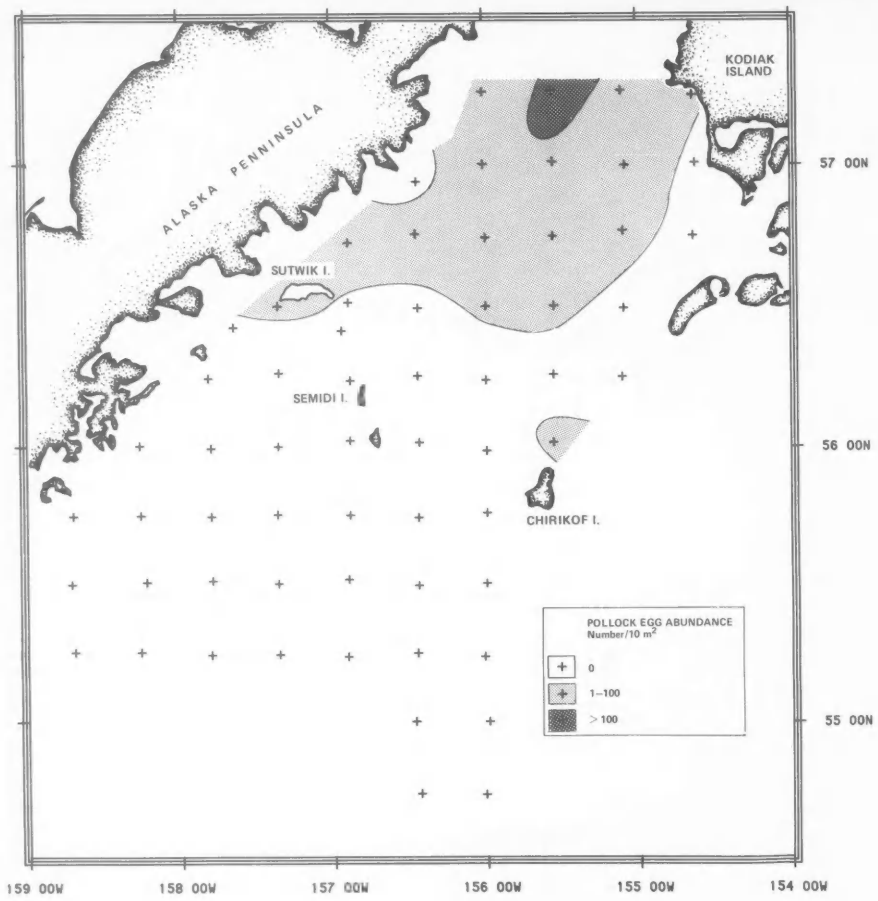

FIGURE 6.—Distribution and abundance of walleye pollock eggs, May 1983.

(Table 2). The means of the catch per 10 m^3 at each time-depth combination expressed as a percentage of the total catch at that time of day suggests a pattern of limited diel vertical migration (Fig. 7). The chi-square test was highly significant ($P < 0.005$) indicating that the null hypothesis, that the larvae were distributed at each depth in the same proportions among the different times, should be rejected. Examining the relative abundances within each time period, the larvae appeared to be concentrated above 20 m at 0630 h, and at 28-47 m by 1830 h (Fig. 7). They were most evenly distributed in the early afternoon and most abundant in the 21-28 m stratum during darkness (2230 and 0230 h) and at 1030 h. The lowest percent abundance at each time period shows a complementary pattern, with relatively small catches at 39-47 m from 0230-1430 h. This pattern was observed on both days during the 48-h sampling.

In summary, it appears that some larvae gradually move up in the water column from a depth of 30-50 m in the evening to above 20 m in early morning. They gradually descend during daytime, and are most evenly distributed in the early afternoon.

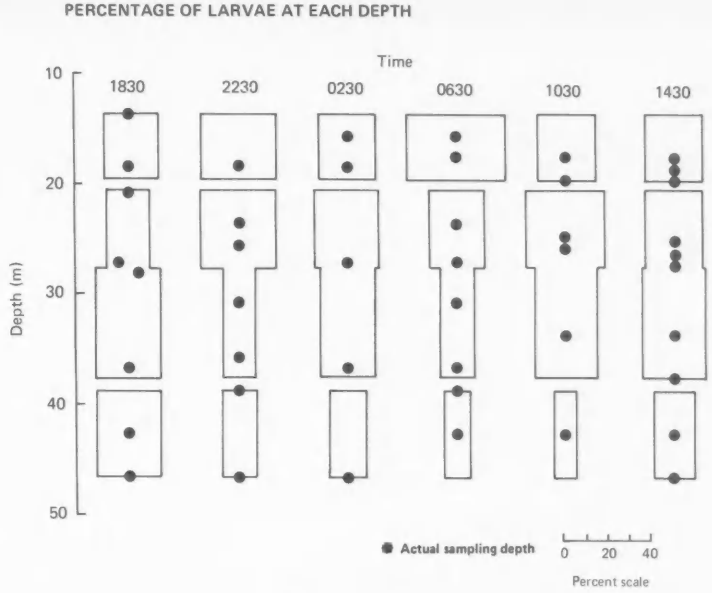

FIGURE 7.—Relative abundance as percent of larvae at each depth for each time interval, of walleye pollock larvae from the vertical distribution study, May 1983.

Comparison of Catches of Walleye Pollock Larvae by Different Gears

The sizes of larvae in the different bongo nets at the vertical distribution station were similar (Table 3). Mean lengths of larvae in the 20 cm bongo nets varied from 11.00 in the 333 μm mesh net to 11.10 mm in the 253 μm mesh net (SD = 1.76 and 1.69 mm respectively); mean length in the 60 cm bongo nets was 11.07 mm (SD = 1.77 mm). The Tucker trawl, however, caught larvae that had a mean length of 9.64 mm (SD = 1.67 mm). The overall mean abundance of larvae in the 20 cm bongo in the 28-38 m depth stratum nets (11.82 larvae/10 m^3) was similar to that in all the Tucker trawls (11.66 larvae/10 m^3) which were towed at 35 m. The mean of the catches in the 60 cm bongo nets, towed just below the deepest 20 cm bongo, was not notably different from the mean of those 20 cm bongo catches taken at the same times.

Variations in overall catches in the 20 cm bongo nets at the vertical distribution stations seemed to reflect the patchy nature of the concentration of larvae and not net avoidance related to time of day. The largest catches occurred during daylight, at 1030 h, while the smallest catches occurred during the time intervals immediately preceding (0630 h) and immediately following (1430 h) the largest catches. Since we sampled one geographic site rather than following a drogue, we probably sampled water with different concentrations of larvae as it drifted past us during the 48-h sampling. It appears that the larvae decreased from a concentration greater than 1 m^{-3} during the first 24 hours to <0.5 m^{-3} during the second 24 hours. The size of larvae did not change during the study again indicating that increased daytime net avoidance was not significant.

Hydrography in Relation to Distribution of Walleye Pollock Larvae

No obvious hydrographic features were associated with larval distributions. At the diel station, larvae were concentrated between 14 and 47 m where temperature within the upper 50 m was

TABLE 3.—Comparisons of catches and lengths (mm SL) of walleye pollock larvae with gear, time of day, and depth from the vertical distribution study, May 1983.

	mm SL (SD)	number	mm SL (SD)	number
	333 μm mesh		253 μm mesh	
Depth (m)				
14-19	11.13 (1.80)	333	10.86 (1.77)	333
21-28	11.07 (1.74)	405	11.07 (1.87)	427
28-38	11.24 (1.68)	232	11.04 (1.73)	290
39-47	11.19 (1.60)	249	11.17 (1.46)	229
Time (local)				
1830	11.03 (1.67)	210	10.86 (1.65)	118
2230	10.98 (1.58)	189	10.76 (1.56)	185
0230	11.50 (1.83)	315	11.39 (1.75)	361
0630	11.12 (1.42)	133	11.31 (1.82)	116
1030	11.01 (1.75)	331	10.61 (1.81)	301
1430	10.73 (1.57)	183	11.13 (1.72)	182
Gear				
20 cm bongos, 253 μm mesh	11.10 (1.69)	1,388		
20 cm bongos, 333 μm mesh	11.00 (1.76)	1,381		
All 60 cm bongos	11.07 (1.77)	578		
All Tucker trawls	9.64 (1.67)	2,180		

stable at 6.90°-6.15°C (Fig. 8). Nearby, salinity and density showed a very gradual increase with depth.

The pattern of water movement in the survey area, derived from the temperature and salinity observations, indicated a general southwest flow of water at all depths. In the area of larval concentration, most of the flow tended southward, following the deep trough from Shelikof Strait across the continental shelf between the Semidi Islands and Cherikof Islands (S. Kim[9]).

Diet and Feeding of Walleye Pollock Larvae

Eighteen different food items were identified in walleye pollock larvae sampled at the diel sta-

[9]S. Kim, School of Fisheries, University of Washington, Seattle, WA 98195, pers. commun. September 1985.

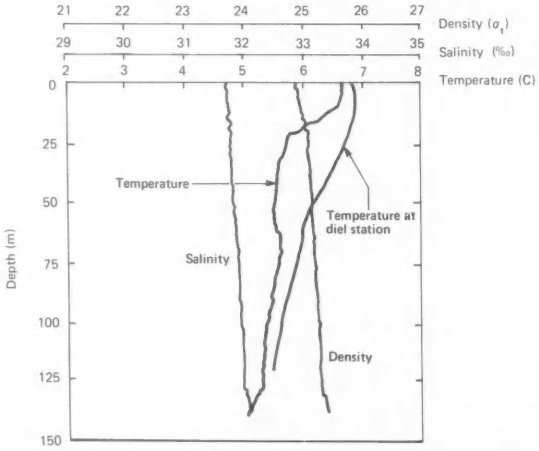

FIGURE 8.—Temperature, salinity, and sigma-*t* profiles at Station 47 with temperature profile from the diel station (Stations 63-77) shown for comparison. See Figure 2 for station locations.

tions. Copepod nauplii 90-600 μm in length and between 40 and 250 μm in width were the most abundant food item for larvae <14.0 mm (Fig. 9). The length- and width-frequency distributions of nauplii indicate that *Pseudocalanus* spp. and *Oithona* spp. are the likely prey taxa. Nauplii became numerically less important in diets of larger larvae. *Pseudocalanus* spp. copepodids, copepod eggs, and *Oithona* spp. copepodids made up a larger numerical portion of the food of these larger larvae (Fig. 10). The increased importance of *Pseudocalanus* spp. copepodids in the diet of larger larvae is evident in terms of gut volume (Fig. 10). Examination of the contribution of the copepod eggs to the diet indicates that while eggs increase numerically from 1.5% in the 8.0-8.9 mm size group to 55% in the 14.0-14.9 mm size group, their volume increases only from 0.5 to 3.6%.

The number of food organisms and mean prey volume per larva show a diel feeding pattern (Fig. 11). The maximum gut contents were observed during the afternoon. Collections at 2235, 0230, 0238, and 0629 have the lowest mean number of food items per larva, which suggests that feeding during darkness is reduced. The mean gut volumes show a similar pattern (Fig. 11). Although gut volume at 1047 h on 29 May was unusually low, it was not an indication of reduced feeding. Here the gut contents consisted of numerous copepod nauplii and few adult copepods. Thus the calculated prey volume is quite low, while the number of food items per gut is high.

Zooplankton Composition

Thirty-nine groups of zooplankters were identi-

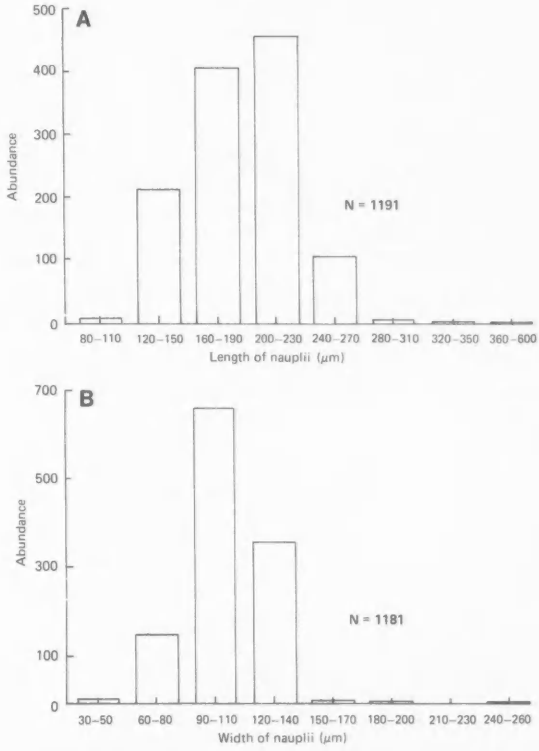

FIGURE 9.—Length (A) and width (B) size-frequency distribution of copepod nauplii from guts of walleye pollock larvae.

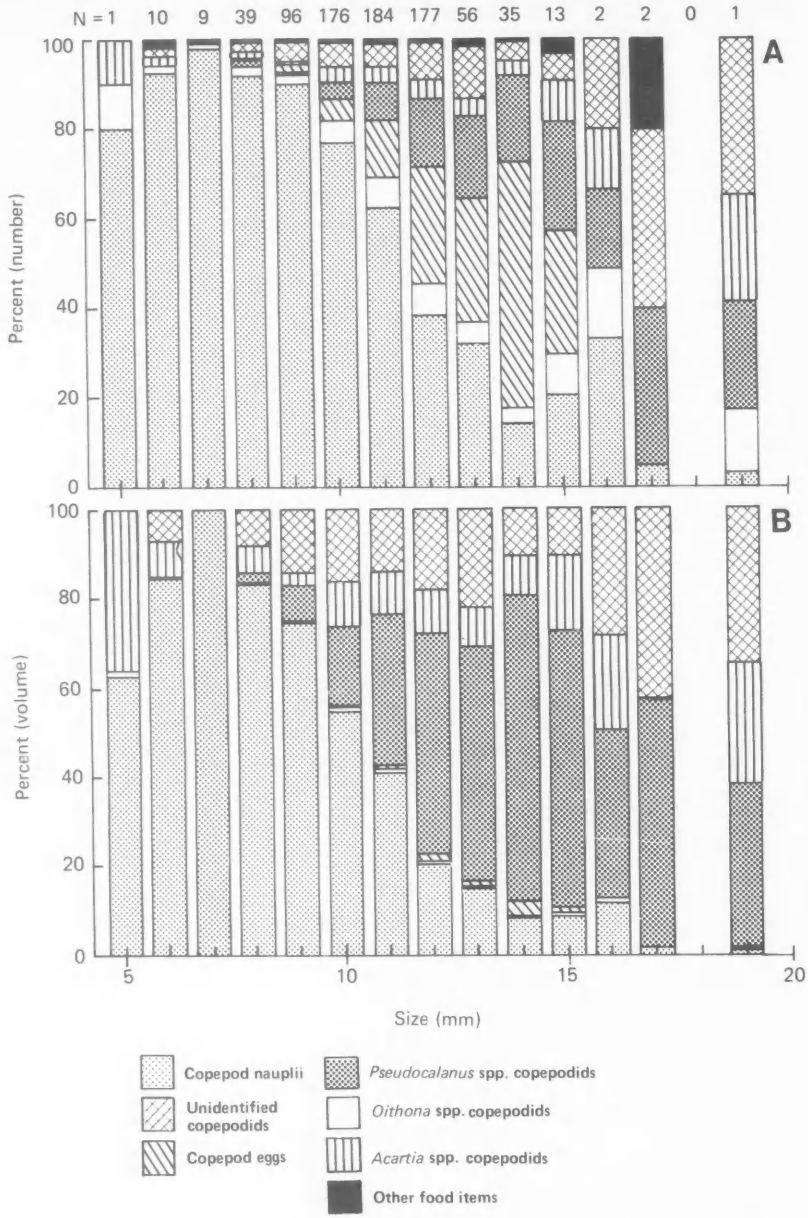

FIGURE 10.—Gut contents of walleye pollock larvae by 1 mm length intervals (5-20 mm) from northern Gulf of Alaska, May 1983. A—percent number; B—percent volume.

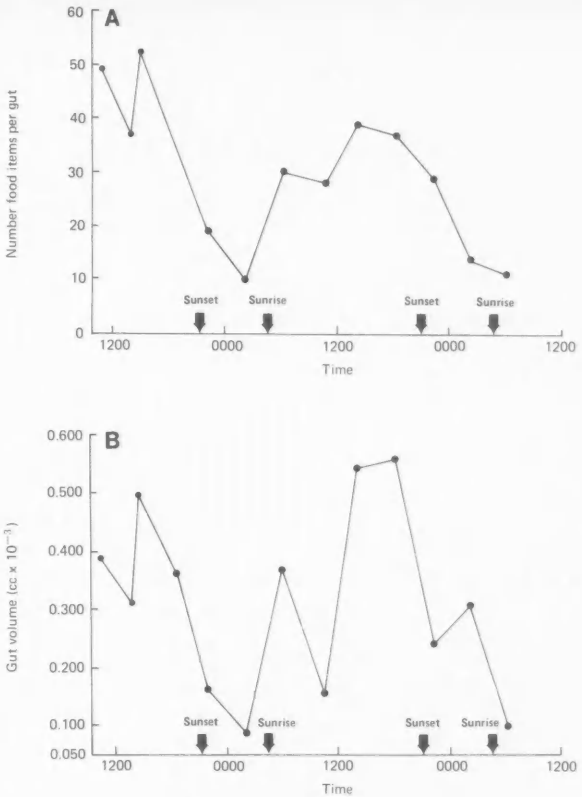

FIGURE 11.—Numbers of prey (A) and gut fullness (B) of walleye pollock larvae by time of day and depth from the vertical distribution stations, May 1983.

fied from samples taken with the 253 μm mesh net (Table 4). *Pseudocalanus* spp. were generally the most abundant taxon. Abundances of *Pseudocalanus* females ranged from 11 m^{-3} to a peak of 1,398 m^{-3} at 1515 h on the first day at a depth of 47 m. The overall mean abundance of *Pseudocalanus* females was 224 m^{-3}. These females comprised between 9 and 23% of the total zooplankton at all depth strata both during the daylight and darkness (Fig. 12). The highest percent contribution by this stage (22-23%) was during daylight hours at the two deepest strata. Peak abundances usually occurred at depth strata below 25 m. Copepodid stages of *Pseudocalanus* also reached a peak of 1,890 m^{-3} at the same station. These copepodids contributed the greatest percentage (21-33%) of the total zooplankton at all depths and times. There were no obvious patterns associated with depth or time of day in either abundance or percent composition of the total zooplankton.

Oithona spp. were abundant in the samples even though they were not collected quantitatively in the 253 μm mesh net. The peak abundance observed was 1,323 m^{-3}. *Oithona* spp. were most abundant in the surface stratum comprising 18% of the total zooplankton during the day versus <10% of the zooplankton at deeper strata during the day and at all depths during the night (Fig. 12). *Acartia* spp., *Neocalanus* spp., and *Calanus* spp. were the only other abundant copepods. The *Neocalanus* spp. and *Calanus* spp. in-

TABLE 4.—Species composition of zooplankton samples from the vertical distribution stations.

Taxon				
Number (See Fig. 11)	Name	Maximum No./10 m^3	Minimum No./10 m^3	Mean No./10 m^3
1	*Pseudocalanus* spp. adult female	13,981	118	2,245
2	*Pseudocalanus* spp. adult male	4,711	0	567
3	*Pseudocalanus* spp. copepodids 1-5	18,915	46	3,592
4	*Neocalanus* spp. and *Calanus* spp.	12,163	0	1,545
5	*Oithona* spp.	13,234	0	1,167
6	*Acartia* spp.	2,476	101	794
7	*Centropages* spp.	380	0	50
8	*Metridia* spp.	—	0	—
9	*Eucalanus bungii*	192	0	7
10	*Paracalanus* sp.	46	0	5
11	*Clausocalanus* sp.	25	0	1
12	*Tortanus* spp.	7	0	—
13	Unidentified calanoid	201	0	9
14	Euphausiid furcilia	3,431	0	511
15	Euphausiid calyptopsis	97	0	7
16	Euphausiid crytopsis	—	0	—
17	*Thysanoessa inermis* furcilia	1,307	0	517
18	*T. inermis* calyptopsis	—	0	—
19	*T. inermis* crytopsis	97	0	5
20	Euphausiid juveniles	—	0	—
21	*T. inermis* juvenile	73	0	5
22	Chaetognatha	592	0	94
23	Appendicularia	1,088	0	290
24	Hyperidae	183	0	31
25	Gastropoda	484	0	62
26	Decapoda	262	0	24
27	Balanidae	253	0	39
28	Gammaridae	7	0	—
29	*Evadne* spp.	97	0	3
30	*Limacina* spp.	1,569	0	364
31	Pontellidae	19	0	—
32	Thecosomata	255	0	21
33	Brachyura	292	0	34
34	Gymnocomata	38	0	1
35	Echinodermata	1,511	0	117
36	Hydrozoa	311	0	18
37	Pelecypoda	28	0	1
38	Medusa	14	0	—
39	Siphonophore	8	0	—

cluded *N. plumchrus*, *C. pacificus*, and *C. marshallae*. Together these species contributed between 13 and 25% of the total zooplankton (Fig. 12).

Euphausiids were the only other abundant group of zooplankters; furcillae were the most abundant stage. The abundance of furcillae was generally <200 m^{-3}; however, at 1047 h on 29 May, the numbers of furcillae exceeded 1,300 m^{-3}.

Age and Growth

Ages were determined for 109 walleye pollock larvae, including 40 individuals collected from Station 37 within the area of highest larval abundance and 69 specimens from four stations well removed from this area. Standard lengths ranged from 6.0 to 14.6 mm and mean increment counts (days since hatching) ranged from 7 to 45.5 (Table 5). The average growth rate varied from 0.12 to 0.25 mm/day among the five stations (Table 5). When compared pairwise with growth rates from all other stations, growth rates from all stations located outside the dense patch, ex-

TABLE 5.—Average growth rates, statistics on the linear regression, comparison lengths, and ages of larval walleye pollock used in growth analysis from five areas in the Shelikof Strait. Station 37 is in the area of highest larval density (Fig. 1).

Station	*Y*-intercept (mm)	*b*-growth (mm d^{-1})	r^2	*N*	No. of fish aged	Length range (mm)	Age range (days)
37	3.7	0.24	0.82	40	40	6.8-13.1	12-42
53	4.2	0.23	0.81	20	20	7.6-13.0	20-41
9	3.5	0.25	0.81	20	20	6.0-14.6	7-43
6	4.7	0.18	0.61	20	20	6.6-12.3	10.6-42.2
12	6.6	0.12	0.90	9	9	8.1-12.6	14-45.5

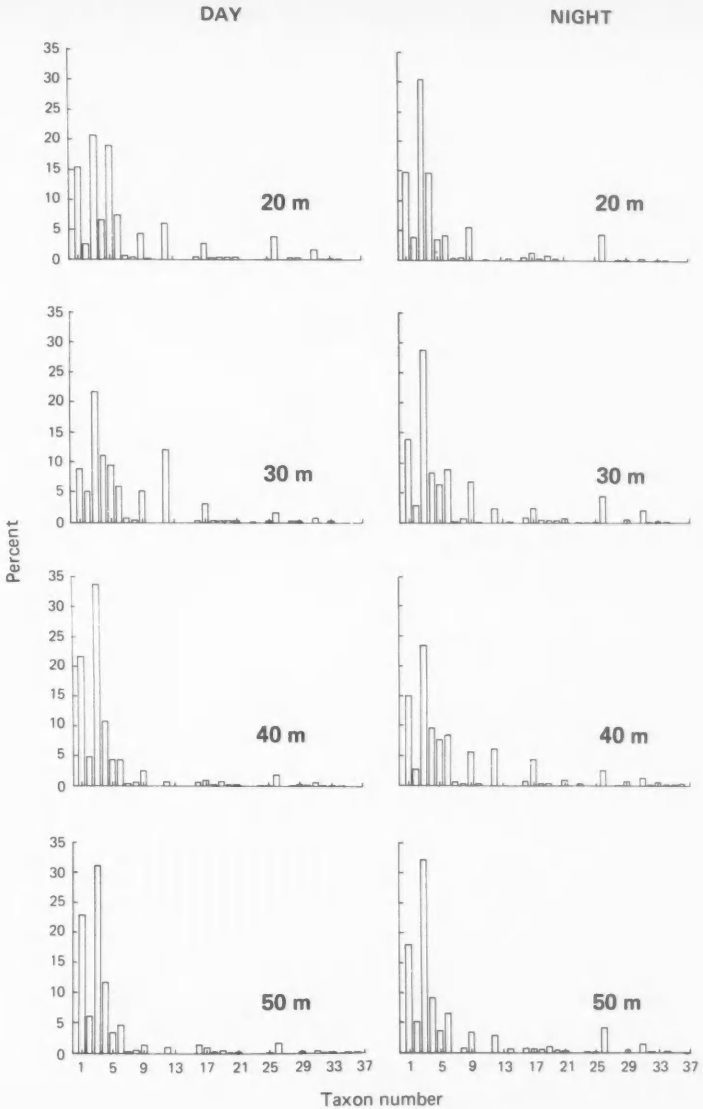

FIGURE 12.—Zooplankton distribution (percent total zooplankton) for day and night by depth from the vertical distribution stations, May 1983. Taxon numbers: 1: *Pseudocalanus* spp., adult female; 2: *Pseudocalanus* spp., adult male; 3: *Pseudocalanus* spp., copepodids 1-5; 4: *Neocalanus* spp. and *Calanus* spp.; 5: *Oithona* spp.; 6: *Acartia* spp.; 7: *Centropages* spp.; 8: *Metridia* spp.; 9: *Eucalanus bungii;* 10: *Paracalanus* sp.; 11: *Clausocalanus* sp.; 12: *Tortanus* spp.; 13: Unidentified calanoid; 14: Euphausiid furcilia; 15: Euphausiid calyptopsis; 16: Euphausiid crytopsis; 17: *Thysanoessa inermis* furcilia; 18: *T. inermis* calyptopsis; 19: *T. inermis* crytopsis; 20: Euphausiid juveniles; 21: *T. inermis* juvenile; 22: Chaetognatha; 23: Appendicularia; 24: Hyperidae; 25: Gastropoda; 26: Decapoda; 27: Balanidae; 28: Gammaridae; 29: *Evadne* spp.; 30: *Limacina* spp.; 31: Pontellidae; 32: Thecosomata; 33: Brachyura; 34: Gymnosomata; 35: Echinodermata; 36: Hydrozoa; and 37: Pelecypoda.

cept Station 12, were not statistically different from growth measured within the dense patch (Station 37). Larvae collected at adjacent Stations 6 and 12, located to the northeast of the densest area (Fig. 2), exhibited the lowest growth rates and were not statistically different from each other.

Estimated age-at-length data from all stations were combined to describe early growth in walleye pollock from the Shelikof Strait region as follows:

$$SL = 4.29 + 0.21 \text{ (age, d)} \qquad n = 109,\ r^2 = 0.75$$

where SL = standard length (Fig. 13). This relationship suggests a mean growth rate of 0.21 mm/day and an intercept of 4.29 mm, which corresponds with the known size of newly hatched larvae (Walline 1983; Nishimura and Yamada 1984).

The distribution of dates of hatching was estimated by back-calculating from the ages determined for larval walleye pollock in the Shelikof Strait. The median birthdates from all stations were similar and thus all 109 samples were combined (Fig. 14). The hatching period ranged from early April to mid-May with a mode in the last

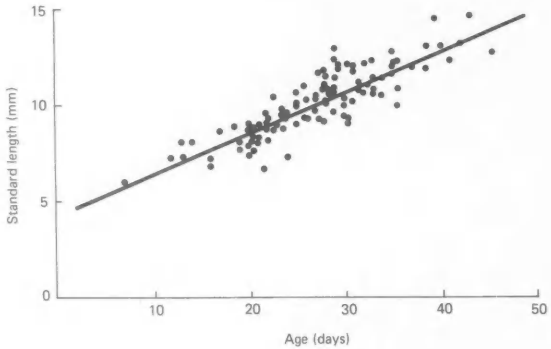

FIGURE 13.—Estimated age at length, fitted with linear regression, for all walleye pollock larvae analyzed from the northern Gulf of Alaska, May 1983.

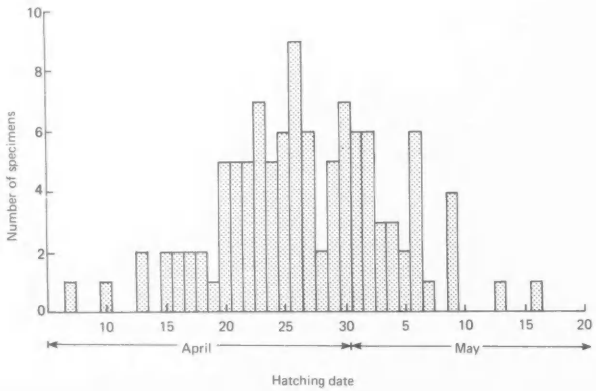

FIGURE 14.—Distribution of hatching dates for walleye pollock determined by back-calculation using age and date of collection.

week of April. Incubation time for walleye pollock eggs held at 5°-6°C in the laboratory is estimated to be 14 days (Haynes and Ignell 1983; Nakatani and Maeda 1984; Nishimura and Yamada 1984); spawning of walleye pollock occurs primarily in late March and early April in Shelikof Strait (Dunn et al. fn. 5), supporting our estimated hatching dates distribution.

DISCUSSION

Relative Abundance of Eggs and Larvae

Neuston collections in spring in the northern Gulf of Alaska have been reported only for 1978, mainly over the shelf, south and east of Kodiak Island, a month earlier than the present study (Kendall and Dunn 1985). Eggs of *Theragra chalcogramma* were most abundant; the rest of the identified eggs were of several pleuronectids. The greater abundance of *T. chalcogramma* in relation to the pleuronectids in the earlier cruise, when compared with the present data (Fig. 5), probably reflects the seasonal difference in spawning times. Pleuronectids spawn mainly in late spring and early summer in the Gulf of Alaska while *T. chalcogramma* is mainly a late winter-early spring spawner (Kendall and Dunn 1985).

Eggs have been reported from bongo catches from three other cruises in the northern Gulf of Alaska in May (Bates and Clark 1983[10]; Kendall and Dunn 1985); eggs of pleuronectids and those of *T. chalcogramma* were most abundant. However, the rank order of abundance of the various pleuronectids varied considerably among the cruises. Usually eggs of *Glyptocephalus zachirus*, *Hippoglossoides elassodon*, and *Microstomus pacificus* were among the five most abundant taxa.

Among larvae in the neuston tows during the present study, mainly spring spawning taxa (e.g., *Ammodytes hexapterus*, *Bathymaster* spp., *T. chalcogramma*) were represented; whereas larvae of fall-winter spawning taxa (e.g., three hexagrammids, and *Hemilepidotus* spp. [Irish lords]) were abundant during the earlier cruise (Kendall and Dunn 1985).

In bongo catches during other May cruises in the area, larvae of *T. chalcogramma*, *Hippoglossoides elassodon*, *Bathymaster* spp., and *A. hexapterus* have always occurred frequently, as in the present study (Bates and Clark fn. 9; Kendall and Dunn 1985).

Distribution of Walleye Pollock Eggs

The few eggs collected during the present study represented a very late part of the spawning, which occurs in Shelikof Strait mainly in early April (Dunn et al. fn. 5) (Fig. 1). Recently hatched larvae (<5 mm SL), which were collected during our survey (Fig. 2), also indicate prolonged spawning but probably at a low level after mid-April. The eggs we found were mainly over the deep waters at the southwest end of Shelikof Strait, and it would be expected that they were also farther to the northeast. This is the same area of occurrence of eggs during the height of spawning (Dunn et al. fn. 5), indicating that the adults spawn mainly in Shelikof Strait throughout this period, although individual spawning fish probably migrate in and out of the area.

Comparisons of Distribution of Walleye Pollock Larvae

In 1981, several sequential cruises to Shelikof Strait mapped a large concentration of walleye pollock eggs in early April; and in late April and again in mid-May, a concentration of larvae was found progressively further to the southwest of the area where the eggs had been (Bates and Clark fn. 10) (Fig. 1). The size of the larvae in the concentration increased between the cruises.

Sampling in 1981 and 1982 for walleye pollock larvae was at the same area and time (24-28 May) as the present study (Dunn et. al. fn. 5). Comparisons of distribution, abundance, and size of the larvae among these 3 years reveal remarkable differences (Table 6). Spawning time in 1981, based on ages of eggs caught in early April, and presence of newly hatched larvae in late April, centered around 5-8 April. In 1983, based on birthdate distributions presented here, modal spawning time was also in the second week of April. Sampling in subsequent years has shown a remarkable consistency in spawning place and time (Kendall unpubl. data). By 24-28 May the patch of larvae in 1981 and 1983 had drifted to the same area, just north of Sutwik Island (Figs.

[10]Bates, R. D., and J. Clark. 1983. Ichthyoplankton off Kodiak Island and the Alaska Peninsula during spring 1981. U.S. Dep. Commer., Natl. Mar. Fish. Serv., NOAA, NWAFC Proc. Rep. 83-09, 105 p.

TABLE 6.—Concentrations and lengths of pollock larvae collected 24-28 May 1981, 1982, and 1983 in the patch resulting from the Shelikof Strait spawning (1981 and 1982 data from Dunn et al. text fn. 5).

Year	Cruise	Date (May)	Stations	Larvae m^{-2}	Lengths (mm SL) Mean	SD
1981	4MF81	24	73, 74	2,318	7.36	1.11
	3SH81	25	225	1,285 (mean = 2,040)	7.77	1.18
1982	2DA82	24-28	108, 115, 117, 123, 124, 126	14-38 (mean = 23)	7.74	1.10
1983	1CH83	24, 28	31, 32, 36, 37, 63	104-214 (mean = 151)	11.23	1.65

1, 2). However, the abundance of larvae in 1981 was about 2,000 m^{-2} while in 1983 it was only about 150 m^{-2}. Mean length in 1981 was about 7.5 mm while in 1983 it was 11.2 mm. Since the spawning dates were the same, this would indicate a much slower growth rate (about 0.09 mm d^{-1}) in 1981 than in 1983 (0.21 mm d^{-1}). In 1982 there were fewer larvae (20 m^{-2}) and they were distributed further southwest than in the other 2 years (Dunn et al. fn. 5). These larvae were not different in length from those in 1981 (7.7 mm). The position of the larvae in 1982 suggests a much faster drift than in 1981 and 1983.

Although most of the spawning occurs in the deep trench (>200 m) in Shelikof Strait, the larvae are in the upper part of the water column. Southwest of Shelikof Strait the trench runs south between the Semidi Islands and Chirikof Island (Fig. 2). Early larvae drift in the Alaska Coastal Current which flows southwest, parallel to the Alaska Peninsula (Schumacher and Reed 1980). At the time of our surveys in May 1981 and 1983, larvae had drifted to the area between Sutwik Island and the Semidi Islands. In 1982 they were further to the southwest in water over the deeper trough and the continental shelf.

Vertical Distribution of Walleye Pollock Larvae

Vertical distribution of walleye pollock larvae has been addressed in detail in several other studies (Kamba 1977; Cooney et al. 1978; Walline 1981[11]; Dagg et al. 1984). Although the areas of study, procedures, and gear have varied, a consistent pattern of diel-vertical distribution emerges from these studies and is supported by the present study. Haryu (1980) summarized his and earlier work by stating "larvae inhabit the mid-layer rather than the surface layer and perform diurnal vertical migration in search of food." Most larvae have been found between 10 and 60 m, and within this depth range, some larvae generally move to shallower depths at night. Vertical movement is not pronounced in any of the studies but is evident by comparing proportions of larvae at various sampling depths at different times of day. In general it appears that larvae <15 mm are most concentrated vertically at 10-15 m at twilight, both in the evening and morning. During nighttime and daytime the larvae are more dispersed vertically, and during daytime their distribution is deeper than at night. Samples confined to day and night periods do not show the crepuscular nature of the distribution. This pattern is seen in the present study but is less pronounced than in some others, possibly because we conducted our sampling only in the vertical range of high concentration. Larvae larger than about 15 mm appear able to avoid plankton nets to some extent, particularly during daytime. The available data, however, suggest that these larger larvae remain concentrated in a shallow depth stratum (5-15 m) except at night when they are more dispersed vertically and may rise closer to the surface (Walline fn. 11).

Fish larvae of most other species that have been studied also migrate upward in the water column at night (Kendall and Naplin 1981). Some species undergo a much more pronounced vertical migration than is apparent with walleye pollock larvae and may cross much greater temperature gradients than observed here. Similar to walleye pollock, larvae of other fish species are visual feeders, and their vertical movements are probably associated with a diel feeding periodicity. Walleye pollock larvae may move to shallower depths at night to allow more feeding in reduced light. They then may spread downward in the water column during daytime in response to increased light penetration and the distribution of their prey. Too little is known about predation on fish larvae to assess the importance of vertical movements on predator avoidance (see Incze et al. 1984).

[11]Walline, P. D. 1981. Hatching dates of walleye pollock (*Theragra chalcogramma*) and vertical distribution of ichthyoplankton from the eastern Bering Sea, June-July 1979. U.S. Dep. Commer., Natl. Mar. Fish. Serv., NOAA, NWAFC Proc. Rep. 81-05, 12 p.

Feeding of Walleye Pollock Larvae

The diet composition of larval walleye pollock in Shelikof Strait is similar to that described for walleye pollock larvae collected in the southeastern Bering Sea (Clarke 1978) and Uchiura Bay, Hokkaido, Japan (Kamba 1977). Copepod nauplii and copepodids of *Pseudocalanus* spp. were the dominant food items in the guts of 6-20 mm larvae in all these studies. As in this study, copepod eggs were also abundant food items. It is difficult in any of these studies to judge if the eggs were captured as individual food items or along with adult female copepods.

Feeding by larvae in the Gulf of Alaska is highest during daylight hours, as observed in other studies (Kamba 1977; Clarke 1978). Clarke (1978) reported that the few collections made at sunrise had larvae with the lowest feeding incidences. Kamba (1977) also reported that the lowest feeding incidences and the lowest abundance of food in the gut occurred near sunrise.

The high densities of larvae in the Shelikof Strait seem to have little effect on their food habits. *Oithona* spp. are abundant in the Bering Sea, Gulf of Alaska, and Uchiura Bay, Japan, and are intermediate in size between *Pseudocalanus* spp. copepodids and copepod nauplii. *Oithona* are an important component of the diet of pollock larvae in the Bering Sea, accounting for more than 25% of the total number of food items for larvae between 11.8 and 17.7 mm (Clarke 1978), but are rare in guts of larvae collected near Hokkaido (Kamba 1977), and represent <16% of the food items for all size groups in the present study. Kamba (1977) cited the low incidence of occurrence of this food item in larvae collected in Uchiura Bay as evidence of selective feeding by walleye pollock larvae.

The zooplankton species composition in the oceanic and outer shelf regions of the Bering Sea (Cooney and Coyle 1981; Smith and Vidal 1984) is similar to that described for the northern Gulf of Alaska and Ocean Station P (Le Brasseur 1965; Damkaer 1977; Fulton 1983; Miller et al. 1984). The Shelikof Strait species composition is similar to these areas. Our zooplankton sampling did not include copepod nauplii so we cannot assess their abundance. The size distribution of copepod nauplii ingested, however, indicates that *Pseudocalanus* spp. and *Oithona* spp. are the probable sources of the copepod nauplii ingested by larval walleye pollock in Shelikof Strait.

Daily production of copepod nauplii at a single station in the Bering Sea has been estimated to be 27,094 m^{-2}, of which more than 95% was *Pseudocalanus* spp. (Dagg et al. 1984). The abundance of *Pseudocalanus* females ranged from 9.9 to 258.9 m^{-3} ($\bar{x}$ = 87.7). The mean abundance of *Pseudocalanus* females in Shelikof Strait was 244 m^{-3}, or 2.6 times greater than the mean abundance in the Bering Sea. Assuming the same rate of daily production, about 69,000 nauplii m^{-2} would be produced in Shelikof Strait. Mean abundance of walleye pollock larvae where Dagg et al. (1984) performed their study was 6.3 larvae m^{-2}, whereas at the diel station in Shelikof Strait the abundance was 156 m^{-2}, about 25 times greater than in the Bering Sea study. If these larvae ate nauplii at the same rate as those in the Bering Sea, 18.3 per day, they would eat about 24% of the production, as opposed to the <1% in the Bering Sea. Other factors such as the relationship between size of larvae and daily ration need to be investigated before more precise estimates of the impact of larval feeding and the possibility of food limitation can be made. It appears that enough nauplii were being produced to preclude density dependent food restrictions at the larval densities observed in the present study.

Growth of Walleye Pollock Larvae

Growth rates were similar in areas of both high and low density (Table 5, Fig. 13). It cannot be determined from our study whether density-dependent factors modified larval growth; growth variations could be produced by patchy distributions of prey. Walleye pollock larvae have been shown to grow faster in the laboratory at higher food densities (Bailey and Stehr 1986), further, where lower or constant larval densities interact with variable prey density, field studies have shown variability in growth (Govoni et al. 1985). Without knowledge of prey availability at each location, however, it is difficult to discern if high densities of prey coincide with dense patches of larvae. The relatively low growth rates found at two adjacent stations outside the patch (Stations 6, 12; Table 6) might indicate an area of less than adequate prey availability.

Growth rates for fishes can be influenced by environmental factors such as temperature, as well as availability of adequate food supplies (Boehlert and Yoklavich 1983). Within species,

growth rates are usually positively correlated with temperature over the normal temperature range. Growth rate for larval walleye pollock in the Gulf of Alaska (0.21 mm d^{-1}) is considerably lower than that determined for larvae of the same size range (4-25 mm SL) collected in the southeastern Bering Sea in June-July 1979 (0.35 mm d^{-1}, Walline 1985). Water temperatures were similar in both studies (about 6°-8°C). Maximum growth determined for larvae collected in the Bering Sea in March-June 1980 while water temperature was much cooler (2°-6°C), was 0.22 mm d^{-1} (Clarke 1984). Thus differences in growth rates of larval walleye pollock in the Bering Sea could be due to differences in water temperature, food availability, or a variety of other factors which may affect growth in larvae (Bailey and Stehr 1986). Future research on growth variability in the field should take into account prey availability, temperature, and size-specific mortality rates.

SUMMARY

1. Walleye pollock in the Gulf of Alaska form an intense spawning aggregation in Shelikof Strait in late winter that produces a dense patch of planktonic eggs in early April. Larvae from this spawning can be followed as they develop and are carried by currents to the southwest during spring.
2. In late May 1981, the density of larvae in this patch (>10 m^{-3}) suggested that density-dependent effects on growth and survival might be expected. A field study of larvae in late May 1983 found maximum densities of only 1 larva m^{-3}, and investigated growth and vertical distribution, and feeding in the patch.
3. The larvae were concentrated vertically between about 15 and 50 m, and tended to be in the upper part of this range during night and early morning, whereas they were deeper during the afternoon and evening.
4. Larvae <10 mm fed primarily on copepod nauplii, with copepodids becoming more important in larvae up to 20 mm. Copepodids of *Pseudocalanus* spp. made up a large fraction of the diet of larvae >10 mm. Most feeding occurred during daylight.
5. The copepods *Pseudocalanus* spp., *Neocalanus* spp., *Calanus* spp., *Oithona* spp., and *Acartia* spp. dominated the net zooplankton samples (253 μm mesh net).
6. Growth, based on otolith increments counted on 109 larvae (6.0-14.6 mm) was linear (0.21 mm/day, intercept = 4.29 mm, $r^2 = 0.75$). Growth rates in the area of high abundance were generally not significantly different from those elsewhere.
7. While at the larval densities observed in 1981, density-dependent effects are possible, at the lower densities we observed in 1983 no such effects were expected or indicated in growth rates or diet. Future studies should include direct measurement of copepod naupliar production rates in the areas inhabited by the larvae.

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ASPECTS OF THE BIOLOGY OF THE HAIR CRAB, *ERIMACRUS ISENBECKII*, IN THE EASTERN BERING SEA

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ABSTRACT

The distribution and relative abundance of the hair crab, *Erimacrus isenbeckii*, were determined from data collected during annual summer trawl surveys conducted by the National Marine Fisheries Service (NMFS) in the eastern Bering Sea, 1979-84. The estimated population was about 23 million crabs from 1979 to 1981, but declined sharply to 4.4 million by 1984. The majority (67%) of the population occurred in the Pribilof Islands area. Male crabs occurred at a mean temperature of 3.4°C and depth of 66 m, whereas females occurred at a mean of 2.4°C and 64 m. Females comprised <10% of the catch in NMFS surveys. Over 99% of the females caught were mature, but only eight were ovigerous with from 34,000 to 160,400 eggs. Length-width and length-weight relationships were calculated for males and females. The majority (77%) of *E. isenbeckii* caught during an independently conducted study in May 1983 were found on a mixed sand and shell substrate. Scientific literature (mostly Japanese) was reviewed to provide information on larvae, reproduction, molting, growth, feeding habits, predation, migration, behavior, fishing, and marketing.

The hair crab, *Erimacrus isenbeckii* (Brandt) (Fig. 1), is a medium-sized brachyuran in the family Atelecyclidae. Hair crab have been fished in Japanese and Korean waters for over 60 years (Kawakami 1934), and much literature is available on the biology, distribution, and abundance of the species in those waters. In contrast, fishing for hair crab in U.S. waters began in 1979 (Griffin and Dunaway 1985[3]). The recent development of a U.S. fishery for hair crab and the substantial decline of the eastern Bering Sea (EBS) population from 1981 to 1984 prompted an analysis of hair crab data collected by the National Marine Fisheries Service (NMFS) during the summers of 1979-84. This report presents data on the distribution and abundance of hair crab in the EBS during those years, as well as aspects of ecology, reproduction, molting, and growth. Additionally, we have summarized the literature concerning this species, since most of it is published in Japanese and not easily accessible to English-speaking readers.

REVIEW OF PUBLISHED LITERATURE ON *ERIMACRUS ISENBECKII*

The hair crab has a quadrangular carapace slightly longer than it is wide, and is densely covered with short bristles and sharp granular projections; seven teeth are present on each lateral margin. Chelipeds and walking legs are stout and spiny. The epistome has a nearly straight anterior margin. Rathbun (1930), Sakai (1939), and Kobyakova (1955) described the morphology of adult *E. isenbeckii* in detail. Five zoeal stages and one megalopa stage in the development of this crab are described by Kurata (1963). According to Kurata, the zoeae are relatively large, ranging from 2.7 to 6.5 mm in body length (orbit to midpoint of posterior edge of telson), depending on zoeal stage, and are equipped with a long dorsal spine (1.2-2.8 mm) and prominent lateral spines that are about one-fourth of the length of the dorsal spine. Abdominal margins of the carapace are fringed with setae; abdominal segments possess knobs, spines, and spinules. The megalopa is about 7.2 mm long. The rostrum is short and wide and ends anteriorly in three short teeth. Abdominal segments lack spines.

In the EBS, hair crab occur from the northern

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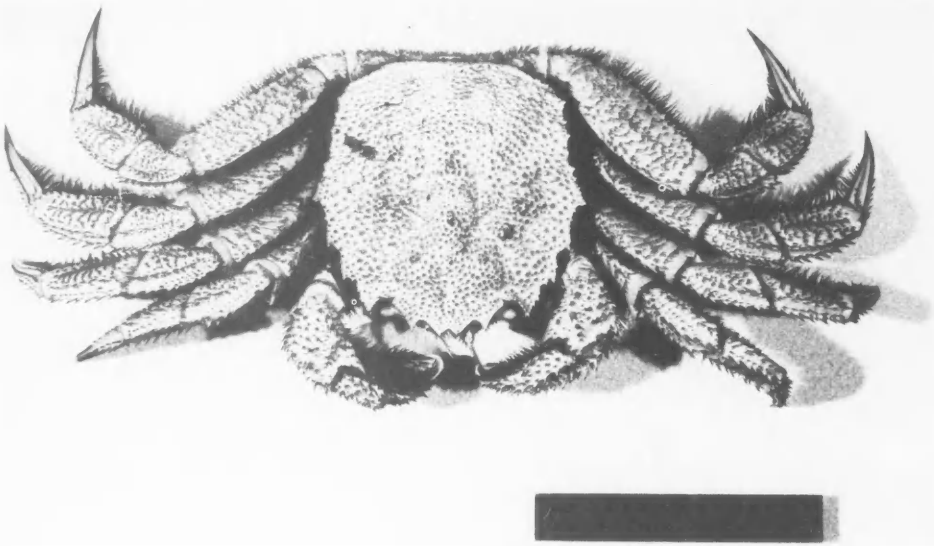


FIGURE 1.—Male hair crab, *Erimacrus isenbeckii*, from eastern Bering Sea. Dorsal view.

shore of the Alaska Peninsula to the Pribilof Islands and St. Matthew Island (Fig. 2). Hair crab are also found along the Aleutian Archipelago from Unimak Island as far west as long. 170°E (west of Attu Island; NMFS unpubl. data). In the western Pacific, hair crab occur along the eastern coast of Korea, the western and eastern coasts of Japan, and southern Sakhalin Island (Rathbun 1930; Tanikawa 1971). They are particularly abundant around the island of Hokkaido and along the Kurile Islands to southern Kamchatka, and are common along west Kamchatka to lat. 54°40′N (Vinogradov 1947). They are unknown from the western Bering Sea.

Dall reported hair crab from Kachemak Bay and Cook Inlet, AK (Rathbun 1930). These, however, were probably *Telmessus cheiragonus*, a similar atelecyclid that commonly occurs in the northern Gulf of Alaska (Calkins 1978), since no verified observations of hair crab have been reported east of Unimak Island despite numerous inquiries to commercial fishermen and biologists working in the northern gulf in recent years.

Sakurai et al. (1972) (Fig. 3, bottom) reported that primiparous (first time breeders) female hair crab off Hokkaido mate from December to February and multiparous (have bred more than once) females mate from August to November (the latter in deeper waters than the former). According to Sakurai et al., mating occurs immediately after molting when females are in the soft-shell condition. When the female is ready to molt, a male crab grasps her chelipeds and holds on to them until after ecdysis. While the female is still soft, the male inserts his copulatory processes into her genital openings and fills the spermathecae with seminal fluid containing spermatophores. The male then secretes a mucoid, proteinaceous substance from his seminal glands which congeals immediately into hard plugs that firmly close the female's genital apertures. The male may then mate with other receptive females. Primiparous

FIGURE 3.—Average molting (top, Abe 1984, see text footnote 13) and breeding (bottom, adapted from Sakurai et al. 1972) cycles of *Erimacrus isenbeckii* (through age 8) offshore of southeastern Hokkaido. It is uncertain when eggs hatch after the second spawning period. Carapace lengths were measured from the notch between the rostral spines. "C" numbers indicate postlarval instars.

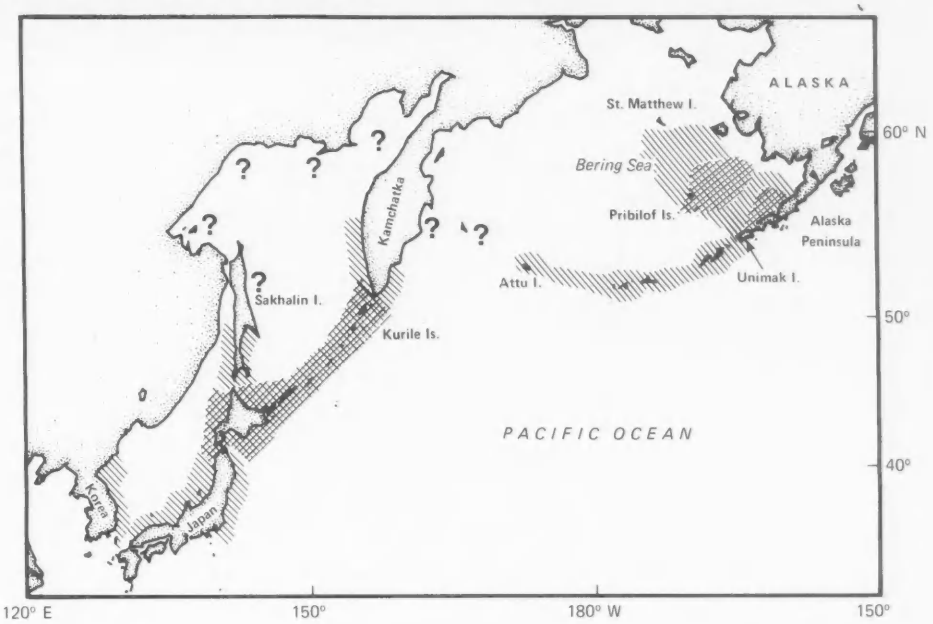
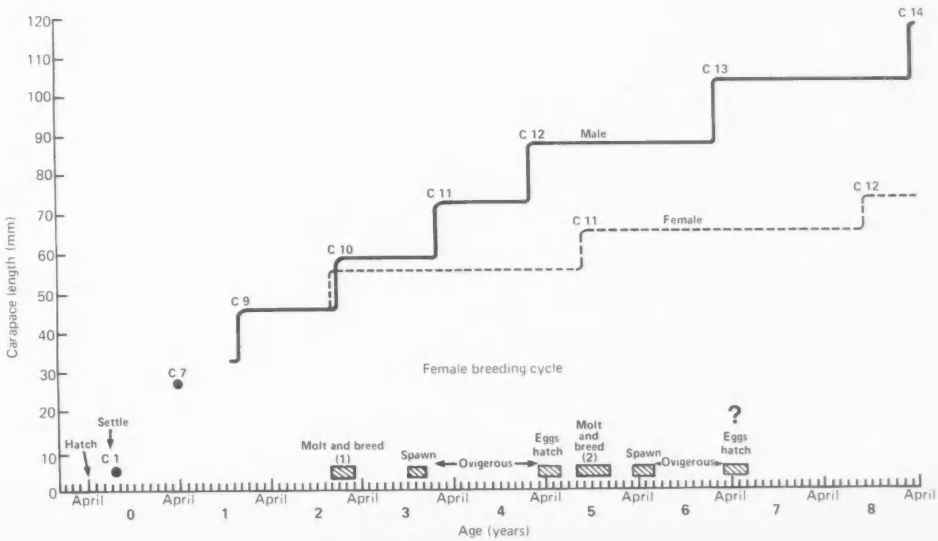


FIGURE 2.—Known world distribution of *Erimacrus isenbeckii*. Areas of high and low density are indicated by crosshatching and parallel lines, respectively. Question marks indicate areas where hair crab are believed to occur but are not well documented.



females extrude eggs in October and November while multiparous females extrude eggs from March to May (Fig. 3) (Sakurai et al. 1972). This indicates a 4-10 mo interval between copulation and extrusion. Yoshida (1940) suggested that spawning occurs only in alternate years.

Oocytes are yellowish white and immature at the time of copulation in both primiparous and multiparous females. During the interval between copulation and extrusion, the oocytes mature into dark orange ova 0.6 mm in diameter (Sakurai et al. 1972). After extrusion, the embryos are carried for at least a year during which time they become dark brown; hatching occurs from about March to May. Sakurai et al. reported that an average of 40,000-50,000 eggs and a maximum of 160,000 eggs were produced and that external embryos were 0.8-0.9 mm in diameter.

The distribution and timing of the occurrence of hair crab larvae near Hokkaido, the Kamchatka Peninsula, and in the eastern Bering Sea have been the focus of several studies. Near Hokkaido, Takeuchi (1969) and Abe (1977) found stages I-III in May and June; stages IV and V in June and July; and megalops from June to August. Takeuchi determined that stages were roughly 2 weeks apart. Stages I and II were only found in the surface layer (0-19 m), whereas stages III-V occurred in the surface and middle (20-50 m) layers. Temperatures ranged from 6° to 11°C at the surface and from 2° to 10°C in the middle layer. Along the West Kamchatka Shelf, stage I larvae were found late-April to May and stages II-V in June and July (Makarov 1967). In the EBS, stages I and II were found late-April to June; stage III, May and June; and stages IV and V and megalops in June (Armstrong et al. 1983[4]). Hair crab larvae in all three geographical areas were concentrated over bottom depths of 20-200 m, although some have been found in waters outside that range.

Abe (1977) reported that settlement of hair crab larvae near Hokkaido occurred in July, in waters 20-50 m deep, 5°-7°C, on sandy mud or fine sand. Juvenile crabs remained in that same general area for the next 1.5 years as they grew from 5.1 mm to about 44.5 mm RL[5] (40.2 mm CL) in eight successive molts. Ovigerous females were found in that habitat during the spring. Adult hair crabs moved offshore during July through September, as nearshore water temperatures gradually increased from 6° to 15°C (Abe 1977). Matui (1970) found adults at depths of 20 m in April to 130 m in autumn, offshore of eastern Hokkaido, but hair crab have been found at depths of 5-364 m in other areas around Hokkaido, the Kamchatka Peninsula, and Korea (Kawakami 1934; Sakai 1939). Hair crab were found on a variety of substrates, including sand, mud, gravel, rock, and broken shells, but sandy mud seemed to be most common (Kawakami 1934; Sakai 1939; Matui 1970; Abe 1977).

After settlement in July, hair crab metamorphose to first postlarval crab instars (C1) with a mean size of 5.2 mm RL (Abe 1977, 1982) (Fig. 3, top). External sex characteristics are evident at stage C2 and a mean size of 7.0 mm RL. By the following April, 12 months after hatching, the crab reach stage C7 at a mean length of 27.4 mm RL. Approximately 33 months after hatching, the crab reach maturity at C10 with a length of 55-60 mm RL (50-54 mm CL) (Abe 1977, 1982); however, hair crab males do not mate until 4 years of age and 70 mm RL (64 mm CL) (Sakurai et al. 1972). The smallest recorded male with mature spermatozoa was 41 mm RL (37 mm CL) (Hirano 1935). Molting frequency and mean carapace length are the same for both sexes through stage C9 (Abe 1977, 1982), however, after maturity males molt more frequently (Sakurai et al. 1972) and show greater growth per molt (Abe 1982) than females. Males begin to molt annually at about 55 mm RL (51 mm CL), once every 1-2 years (tending toward 2) in the size range 89-95 mm RL (81-87 mm CL), and biennially at sizes >100 mm RL (91 mm CL) and growth rate decreases with age (Yamamoto 1971). Males 65-105 mm RL (59-96 mm CL) experience a 10-25%

[4]Armstrong, D. A., L. S., Incze, D. L. Wencker, and J. L. Armstrong. 1983. Distribution and abundance of decapod crustacean larvae in the southeastern Bering Sea with emphasis on commercial species. Final Rep. to Natl. Oceanic Atmos. Admin., OCSEAP contract no. NA81-RAC-00059. Office of Marine Pollution Assessment, Alaska Office RD/MPF24, P.O. Box 1808, Juneau, AK 99802.

[5]Japanese scientists have traditionally measured crab lengths from the notch between the rostral spines ("rostral-length", RL), whereas NMFS scientists measure from the right orbit ("carapace length", CL). We converted rostral lengths to orbit lengths with the following equations, determined for crab in the size range of 40-100 mm CL:

Males:	$CL = -0.81 + 0.921\ RL$	$R^2 = 0.982$	$N = 122$
Females:	$CL = -2.10 + 0.943\ RL$	$R^2 = 0.998$	$N = 8$

These equations have similar slopes but significantly different intercepts ($P < 0.05$). All NMFS crab measurements in this report are carapace lengths (CL). Japanese data are reported in original units (RL) and corresponding carapace lengths are also given for crabs >40 mm CL.

growth rate for carapace length (Yamamoto 1971) and females of 50 mm RL (45 mm CL) an 8-17% growth rate (Sakurai et al. 1972).

Molting periods for adult hair crab vary with sex and locality. In general, males distributed along the coasts of Hokkaido and Korea molt between the months of January and July (Yoshida 1940; Domon et al. 1956; Matui 1970; Sakurai et al. 1972) and females molt during the periods of April to June (Yamamoto 1966) or August to February (Sakurai et al. 1972).

Amphipods, anomurans, and isopods are important food items of the hair crab and peak feeding occurs at midday (Hirano 1935; Sakurai et al. 1972; Abe 1973). Hair crab are prey to fish species including various cottids (Sakurai et al. 1972; Abe 1973, 1982), salmon (Takeuchi 1972), and cod (June[6]), and are occasionally eaten by red king crab, *Paralithodes camtschatica*, (Cunningham 1969).

Hair crab migrate between shallow and deeper waters for mating purposes or in response to temperature changes (Yamamoto 1966; Sakurai et al. 1972). Primiparous females mate nearshore during winter, whereas multiparous females mate in deeper waters during autumn. Juveniles remain nearshore in water temperatures up to 15°C in late summer but adults move offshore. Hair crab also migrate along shore possibly to avoid increased densities (Hirano 1935; Abe 1977). Hirano reported that the longest straight-line migration of a tagged crab was 18 km over a 16-d period and the greatest migration speed was 1.39 km/day; however, the remaining 180 crabs recovered (442 tagged crabs released) within a 48-d period were at the site of release or within 7 km.

Hair crab have been fished in Japanese and Korean waters with the use of conical pots (Fig. 4), trawls, and gill nets (Matui 1970; Yamaha Fishery Journal 1981). In any month of the year fishing occurs at some location around Hokkaido; it occurs from about November to April offshore of southern Hokkaido (Kawakami 1934; Yamaha Fishery Journal 1981) and from March to December offshore of northern Hokkaido (Kawakami 1934; Matui 1970; Tanikawa 1971). Management measures have included area closures, total catch limits, pot limits, legal-size restrictions, and male-only restrictions (Matui 1970; Yamaha Fishery Journal 1981). Hirano (1935) and Kawakami (1934) believed that hair crab are especially vulnerable to fishing pressures owing to "localized" migratory behavior, low number and fecundity of females, and the extended breeding period. By 1980, about 10 t of hair crab were harvested offshore of Hokkaido every day, with 90% of the harvest transported live to fish markets throughout Japan (Iversen[7]), and the remaining 10% sold frozen.

U.S. fishermen began to land hair crab from the EBS in 1979 (Table 1). The majority of the commercial harvest has occurred incidental to snow (Tanner) crab (*Chionoecetes* sp.) fishing in the Bering Sea during the months of March through June, however, fishing season is not restricted. Only male crabs are landed. The Pribilof District (see Results for description of district) contributed 94-98% of the total Bering Sea catch during 1980-84. Harvested crabs averaged 105.7 mm CL and 0.91 kg in 1984. Landings ranged from 2 t in 1979 to a peak of 1,108 t in 1981. Modified, baited king and Tanner crab pots are normally used. Pribilof Islanders, however, conducted an experimental

[6]J. June, Fisheries Research Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. December 1982.

[7]R. Iversen, Regional Fisheries Attache, U.S. Embassy, Tokyo, Japan, APO San Francisco, CA 96503, pers. commun. August 1982.

TABLE 1.—Statistics of the U.S. commercial fishery of *Erimacrus isenbeckii* in the eastern Bering Sea (modified from Griffin and Dunaway, see text footnote 3). Mean length determined from port sampling, mean weight from landing records.

			Crab catch				Crab size	
Year	Vessels	Landings	number (× 1000)	Metric tons	Pots lifted	Crabs/ pot	Mean weight (kg)	Mean length (mm)
1979	11	16	2	2	9,908	0.2	0.95	111.8
1980	9	17	25	24	14,506	1.7	0.95	114.5
1981	67	192	1,127	1,108	172,695	6.5	1.00	104.8
1982	48	159	467	423	117,518	4.0	0.91	103.1
1983	52	161	575	550	84,346	6.8	0.95	103.2
1984	19	74	398	364	42,806	9.3	0.91	105.7

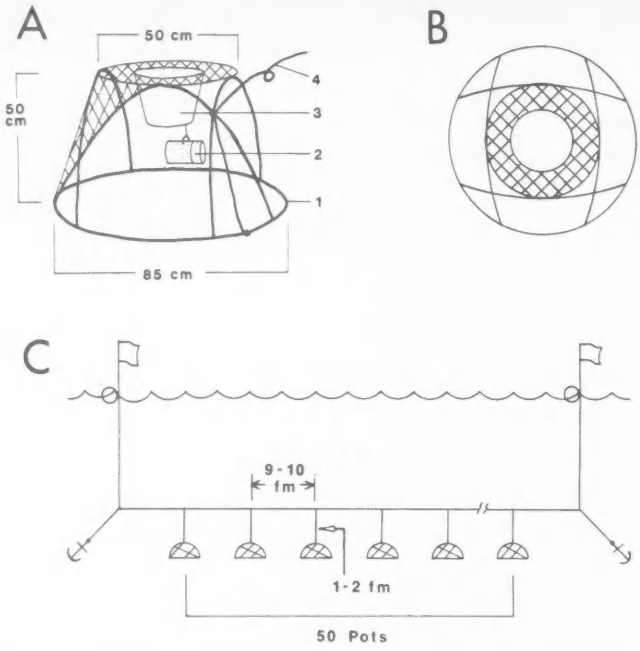


FIGURE 4.—Construction design and fishing method of Japanese hair crab pots. A, Side View: 1, lower ring of steel, upper ring and lateral bars of bamboo; 2, baitcan; 3, polyethylene cylinder entrance (28 cm top diameter, 25 cm bottom diameter, 19 cm high); 4, branch line attached to lateral bars and lower ring. Mesh shown only on top and one side. B, Top view: C, Longline method of pot fishing (fm = fathoms).

fishery for hair crab during the summer of 1980 with the use of small conical crab pots (Merculieff[8]). All hair crab harvested in the United States have been exported to Japan as live or whole-boiled product, and prices to fishermen have ranged from $0.50 to $1.60/lb.

MATERIALS AND METHODS

Hair crab were caught by NMFS during annual summer trawl surveys (primarily designed to assess the abundance of king crab, Tanner or snow crab, and ground-fish species) in the EBS from 1971 to the present, but detailed data on hair crab have been collected only since 1979. Fishing was conducted with a 400-mesh eastern otter trawl in 1979-80 and with an 83-112 eastern otter trawl in 1981-84; effective widths were 12.2 and 15.2 m, respectively (both nets were described by Wathne (1977)). Studies comparing the two nets showed no differences in size selection for king and Tanner crabs. We assumed the same for hair crab, which were too scarce for comparison. These differences in net widths have very minimal effect on the presentation of crab abundance, which is by order of magnitude (0-1, 1-10, 10-100 crab/nmi towed).

In all years, the survey area extended from the Alaskan coast out to approximately the 200 m isobath and included Bristol Bay and the Pribilof Islands area, where hair crab densities are usually greatest (Fig. 5). Only the northern limit of the survey area varied annually. Hair crab were also collected during NMFS cruises to the EBS in February of 1983 and 1985 and during an Outer Continental Shelf Environmental Assessment

[8]Merculieff, L. 1981. Final report on the Pribilof hair crab project. Unpubl. manuscr., 18 p. Tanadgusix Corp., St. Paul Island, AK 99660.

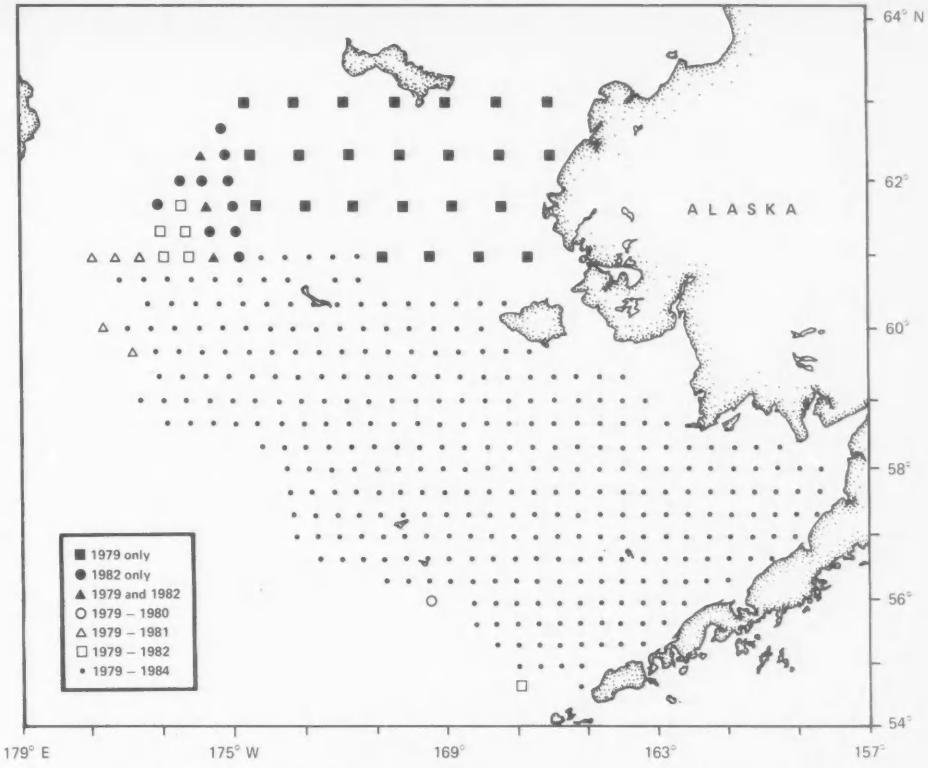


FIGURE 5.—Standard station pattern for NMFS eastern Bering Sea summer surveys, 1979-84. Actual stations occupied may have differed slightly from this pattern in any year.

Program (OCSEAP) cruise to the Pribilof Islands in May 1983. The seasons and durations of cruises are shown in Figure 6. Additional data concerning the NMFS summer cruises is contained in Otto et al. (1985, for the 1984 survey; similar documents are produced annually). Eastern otter trawl gear was used on all vessels throughout the 6-yr study period, except during the May 1983 OCSEAP cruise. On that cruise, either a 3.0 m beam trawl, 7.2 m try-net, or 1.2 m rock dredge were used to collect crabs, depending on bottom type determined from sediment samples taken with a Shipek bottom grab at each station. Fishing during both February cruises and the May 1983 cruise was conducted round-the-clock, whereas that during the summer surveys occurred only during daylight hours. Data collected during the February cruises and May 1983 cruise were not used in this report to determine distribution and abundance of hair crab in the EBS because of the limited area surveyed; only 1979-84 summer survey data were used for that purpose. Because different techniques were involved and no comparative fishing was conducted, catches of hair crab during the May 1983 cruise cannot be compared statistically with those from the summer surveys.

Tows were made in a systematic grid pattern with stations located 37 km (20 nmi) apart. During several years, extra tows were made in areas of higher hair crab abundance around the Pribilofs and in Bristol Bay, which increased the precision of population estimates during those years. Each tow lasted 0.5 hour and most were 2.2-3.3 km (1.2-1.8 nmi) long. Bottom temperatures were recorded with an expendable bathythermograph

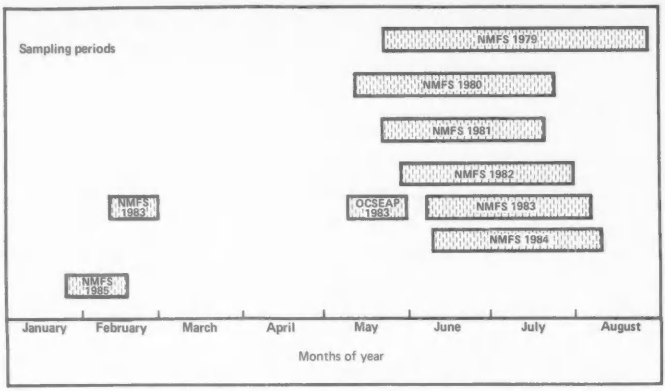


FIGURE 6.—Seasons and durations of sampling periods in the eastern Bering Sea, from 1979 through February 1985.

at as many stations as possible. After the catch was brought aboard, all species including hair crab were removed, counted, and weighed.

Carapace length of each crab was measured with steel vernier calipers to the nearest 1.0 mm from the rear of the right orbit to the middle of the posterior edge of the carapace (carapace length, CL). Carapace width (CW) was measured to the nearest 1.0 mm across the widest part of the carapace, excluding the lateral spines. Crabs were weighed on a triple-beam balance, and weights recorded to the nearest 1.0 g for crabs selected from a stratified size distribution. Shell condition was recorded as follows: molting (Drach's stages D_2 through E; Passano 1960), softshell (stages A_1 through B_1), new hard shell, old hard shell (probably skipped one annual molt), and very old hard shell (probably skipped several annual molts). Hard-shell conditions were graded subjectively according to the amount of epifauna on the carapace, color of carapace, and wear on the spines. A new hard-shelled crab carapace was relatively clean with no epifauna, reddish to yellowish brown, with sharp spines. A very old hard-shelled carapace, however, was usually darker brown in color and almost always had epifauna, and spines that were rounded or worn smooth. An old hard shell was intermediate between these two conditions, but in practice it was difficult to distinguish between new and old hard shell. The presence or absence of external embryos was recorded for all female crabs. Six ovigerous females caught by NMFS in the EBS, 1979-85, were preserved in 10% formalin and returned to the Kodiak NMFS laboratory for determination of fecundity. The entire clutch was removed from the crab, and the embryos dried, sieved to remove debris, and weighed to the nearest 0.1 mg. Three subsamples of embryos from each crab were weighed and counted. The total number of embryos was estimated by dividing the total clutch weight by the average embryo weight. For each of three crabs caught in 1980, diameters of 30 fixed embryos were measured to the nearest 0.1 mm under a stereomicroscope with an ocular micrometer, and average embryo diameters were calculated. Embryos were nearly spherical so no distinction was made between length and width. Other data were analyzed to determine distribution and abundance, sex composition, length frequency, molting periods, relative age according to shell condition, distribution by temperature and depth, and reproductive condition of females.

Population estimates were derived from trawl data using the area-swept technique (Alverson and Pereyra 1969) as described in Otto et al. (1985). The sampling variable was crab density, expressed as crabs caught per unit area swept, the latter equalling the product of net width and distance fished (determined with loran). High- and low-density strata were defined using the cumulative square root of frequencies method (Cochran 1963). Mean, total, and variance of crab density was determined within each stratum, and these combined for extrapolation to the survey area.

RESULTS

Distribution and Abundance

In the EBS, hair crab range from Bristol Bay west to about long. 174°00′W and north to St. Matthew Island at lat. 60°30′N (Fig. 7). Because so few juvenile and female hair crab were caught in NMFS surveys, the following information on distribution and abundance primarily concerns large males. Since fishery landings consist primarily of male crabs >89 mm CL, these are called "large", whereas "small" refers to male crabs <90 mm CL.

Within the survey area, the crabs are divided into eastern and western centers of abundance. The western group occurs primarily in the Pribilof District (Alaska Department of Fish and Game [ADF&G] statistical district; south of 58°39′N, and west of 168°00′W) and is most dense (>10 crabs/nmi trawled) immediately adjacent to the Pribilof Islands. Moderately dense concentrations (1-10 crabs/nmi trawled) surround the Pribilof high-density region, especially to the northeast and south. The eastern group occurs in the Bristol Bay District (south of 58°39′N and east of 168°00′W) and is centered along the northern shore of the Alaska Peninsula from western Unimak Island to about 160°00′W. This group is moderately dense, with areas of high density (10-100 crabs/nmi trawled) located near the western end of the Alaska Peninsula in 1979, and offshore of Unimak Island in 1981. Hair crab are scattered across the continental shelf between these two major population centers and in the Northern District (north of 58°39′N) in low densities (<1 crab/nmi trawled). As with large males, small males and females displayed distinct eastern and western concentrations, but very few were scattered between these two regions. Because of the more-or-less continuous distribution of hair crab across the EBS, we subsequently treat them as belonging to a single widespread population.

Population estimates have been made for hair crab only since 1979 (Table 2), and as previously mentioned, these reflect primarily the abundance of large males. From 1979 to 1981, the estimated population of EBS hair crab remained fairly stable between 22 and 24 million crabs. The population dropped 60% between 1981 and 1982, 35% from 1982 to 1983, and 30% more from 1983 to 1984, to a low of only 4.4 million crabs. (*Note added in proof*: Hair crab abundance has continued to decline to a total of 2.5 million crabs in 1986.) From 1979 to 1984, an average of 67% of the EBS hair crab occurred in the Pribilof District, 27% in the Bristol Bay District, and 6% in the Northern District. Although the total population size did not vary greatly from 1979 to 1981, the proportion of the population in the Pribilof District increased from 51 to 81%, while it decreased from 40 to 18% in the Bristol Bay District, and from 9 to 1% in the Northern District. By 1984, the population distribution was again similar to that of 1979. The population was very densely concentrated around the Pribilofs in 1981; however, since that time, the densities and range of hair crab in the EBS have declined greatly.

Females comprised only 8% (248) of the total catch of about 3,091 hair crab during the 1979-84 NMFS summer surveys. In contrast, females accounted for 40% (48) of the 120 hair crabs >40 mm CL caught during the survey conducted in the Pribilof Islands in May 1983, when fishing was conducted both day and night around the Pribilof Islands, with dredge, try-net and beam trawl.

Habitat

Male *E. isenbeckii* collected during the summer

TABLE 2.—Population estimates for *Erimacrus isenbeckii*, in the eastern Bering Sea, and proportions of the total population present in each statistical district. See text and Figure 7 for description of districts. Numbers are millions of crabs[1]. M = Male, F = Female.

	Pribilofs				Bristol Bay				Northern				Totals				Grand
Year	M	F	All	%	M	F	All	%	M	F	All	%	M	±%[2]	F	±%	total
1979	11.9	0.3	12.2	51	8.8	0.9	9.7	40	1.8	0.4	2.2	9	22.5	29	1.6	35	24.1
1980	15.1	2.3	17.4	77	3.6	0.7	4.3	19	0.8	0.1	0.9	4	19.5	47	3.1	138	22.6
1981	18.1	0.3	18.4	81	3.7	0.5	4.2	18	0.2	0.0	0.2	1	22.0	19	0.8	42	22.8
1982	6.3	0.1	6.4	67	2.3	0.2	2.5	26	0.5	0.1	0.6	6	9.1	22	0.4	56	9.5
1983	2.8	0.3	3.1	48	1.9	0.5	2.4	39	0.7	0.1	0.8	13	5.4	15	0.9	38	6.3
1984	2.3	0.2	2.5	57	1.2	0.1	1.3	30	0.5	0.1	0.6	13	4.0	16	0.4	48	4.4

[1]Numbers represent only crabs within the survey area and those large enough to be retained by the trawl, i.e. mostly large males (>89 mm CL).
[2]Two standard errors expressed as a percentage of the mean.

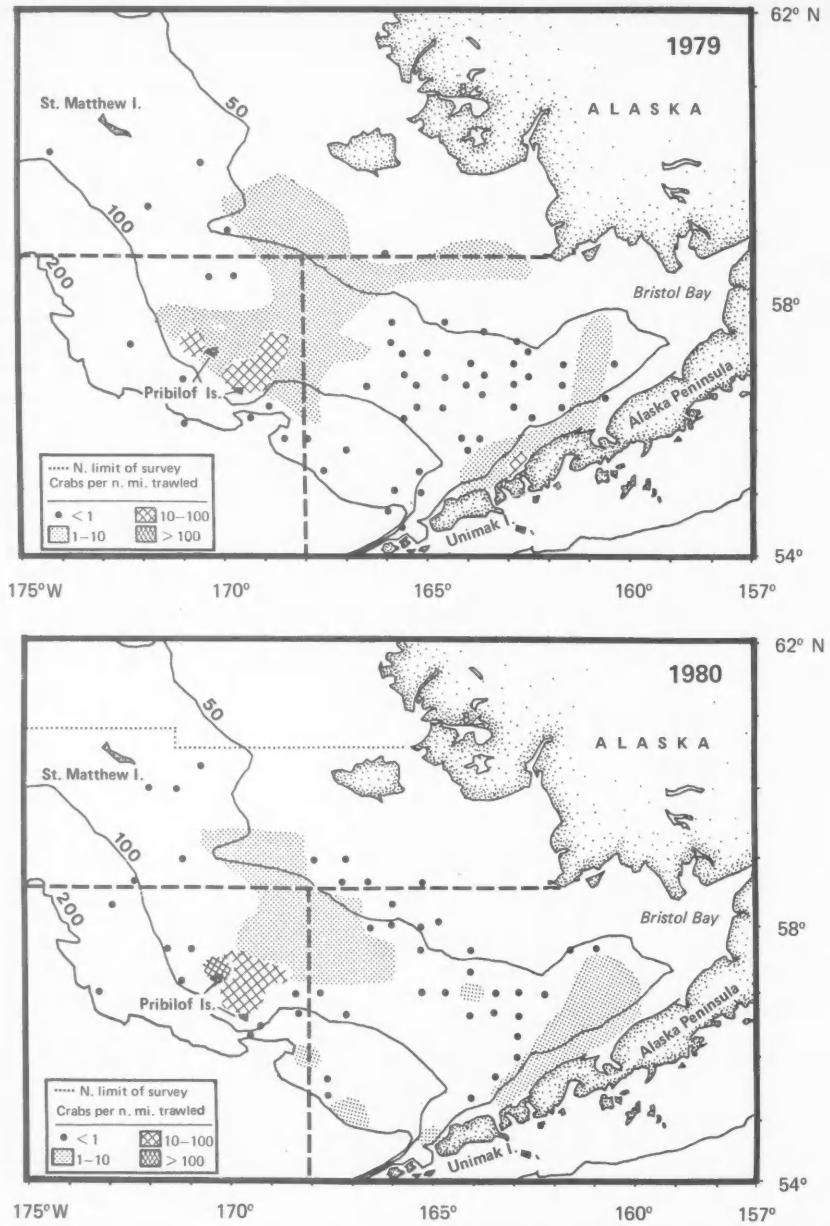


FIGURE 7.—Relative abundance of *Erimacrus isenbeckii* in the eastern Bering Sea, 1979-84. Depth contours are shown at 50, 100, and 200 m. Dotted line indicates the northern limit of the survey in each year. Dashed lines demarcate the Bristol Bay (south of lat. 58°39′N, east of long. 168°00′W), Pribilof (south of lat. 58°39′N, west of long.

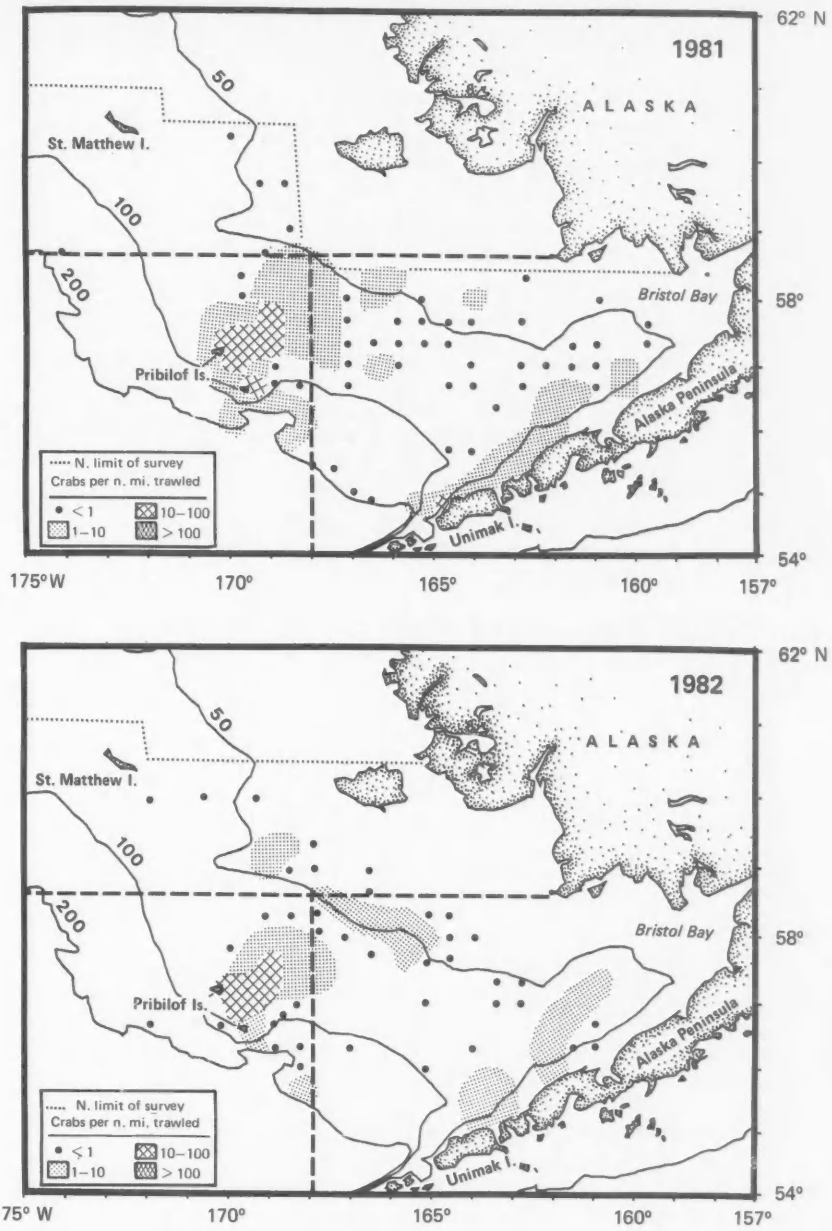


FIGURE 7.—*Continued*—168°00′W), and Northern (north of lat. 58°39′N) statistical districts. Densities expressed as crab per nautical mile trawled.

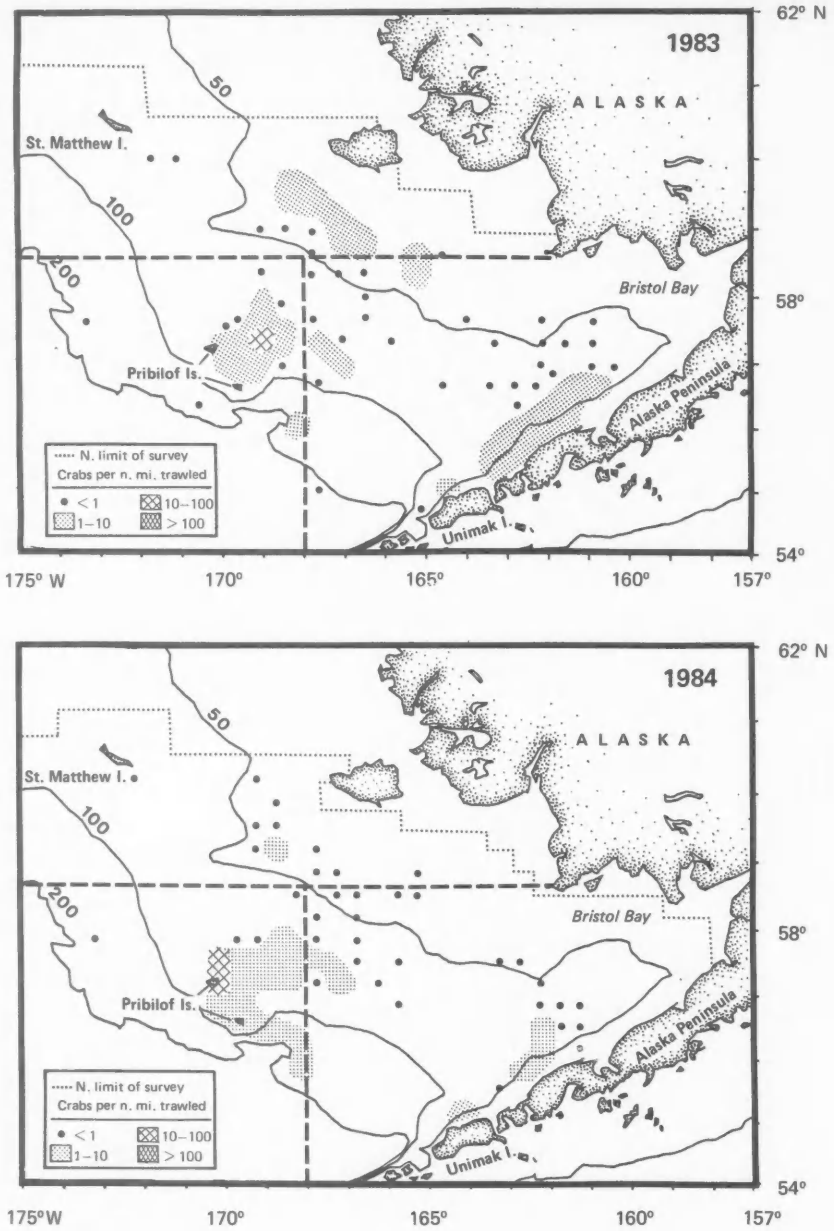


FIGURE 7.—*Continued.*

surveys occurred at a mean temperature (weighted by crab abundance) of 3.4°C and depth of 65.6 m, although they ranged from −0.9° to 10.1°C and from 22 to 249 m depth. One male hair crab was found outside this range, at 401 m. The mean values for females were 2.4°C (range −0.9°-7.3°C) and 63.8 m depth (range 26-243 m). Results of a 2-sample t-test with unequal variances (Minitab "Twosample T" test; Ryan et al. 1976) indicated there was no significant difference ($t = 1.52$, df = 213, $P = 0.13$) between mean depths at which male and female hair crab were found; however, there was a significant difference ($t = 5.82$, df = 219, $P < 0.01$) between mean temperatures.

Data from the Pribilof Island study of May 1983 indicate that hair crab appear to prefer a heterogenous substrate as early juveniles, switching to sandy bottoms with increasing age. Among 120 juveniles <20 mm CL, 41% were on a substrate of gravel (less than about 1 cm diameter), polychaete tubes, and shell fragments, and small numbers were found in areas of large rocks, mud, or large shells. A substrate of medium or fine sand (usually containing shell fragments) was occupied by 58% of crabs in the size range <20 mm CL, 70% of 10 crabs in the range 20-40 mm CL, 94% of 73 males >40 mm CL, and all 48 females >40 mm CL.

Reproduction

The scarcity of juvenile and female hair crabs in NMFS collections prevented a thorough study of reproductive characteristics of the EBS population; only eight ovigerous females were caught from 1979 to 1985. The size at maturity of these crabs in the EBS is unknown, however, the smallest mature female caught by NMFS was 38 mm CL and had spermathecae filled with a viscous liquid, indicating it had been mated. The smallest female with empty egg cases caught by NMFS was a 42 mm CL old hard-shell crab. We follow Abe (1977) in assuming that the mean size at maturity for female hair crab is above 55 mm RL (50 mm CL).

Some female hair crabs collected during NMFS summer surveys were found with hard, proteinaceous plugs in the gonopores. The plugs were root-like in appearance and formed a large, whitish, irregular-shaped protuberance outside the aperture (Fig. 8a). Each plug had a white, tapered stem that extended inward to the spermatheca (Fig. 8b). Some gonopores without plugs were closed by a flexible, swollen membrane (Fig. 8c) similar to the arthrodial membrane and continuous with the lining of the canal leading to the spermatheca. Some gonopores were open (Fig. 8d), owing to the flexible membrane having become flaccid.

Although the presence of closed pores was not associated with any particular shell condition of the female, plugs and open pores were. Plugs were present only in recently molted soft-shell crabs, while most females with open pores (28 of 30, or 93%) were new or old hard-shell crabs. Some females had only one plug, and 96% of these also had the other pore closed. During the May 1983 OCSEAP cruise, 40% (19) of the 48 large females (>40 mm CL) caught had plugged gonopores, 1 had new uneyed embryos, 4 carried eyed embryos that were in the process of hatching, and 11 carried empty egg cases. Of the 19 females with plugged gonopores, 89% (17) were new hard-shell crabs and 2 were newly molted soft-shell crabs.

Most female hair crabs caught carried no external embryos (Table 3A). Although few crabs with

TABLE 3.—Seasonality of egg bearing and molting in *Erimacrus isenbeckii* from the eastern Bering Sea. A) Percent of female crabs (actual number in parentheses) with embryos in each of 4 developmental stages. B) Percent of molting or soft-shelled crabs for each sex (total number of males or females caught shown in parentheses).

	February surveys		Summer surveys, 1979-1984, years combined			
	1983	1985	May	June	July	August
A. Condition of external embryos						
None	86(26)	93(14)	89(16)	88(109)	73(54)	38(12)
Uneyed	0	7(1)	0	0	1(1)	3(1)
Eyed	7(2)	0	11(2)	1(1)	0	0
Hatched	7(2)	0	0	11(14)	26(19)	59(19)
B. Frequency of molting or soft-shell crab						
Male	20.0(136)	0.0(56)	1.3(234)	2.0(1240)	3.1(1215)	0.0(154)
Female	30.0(30)	6.7(15)	0.0(18)	5.6(124)	18.9(74)	3.1(32)

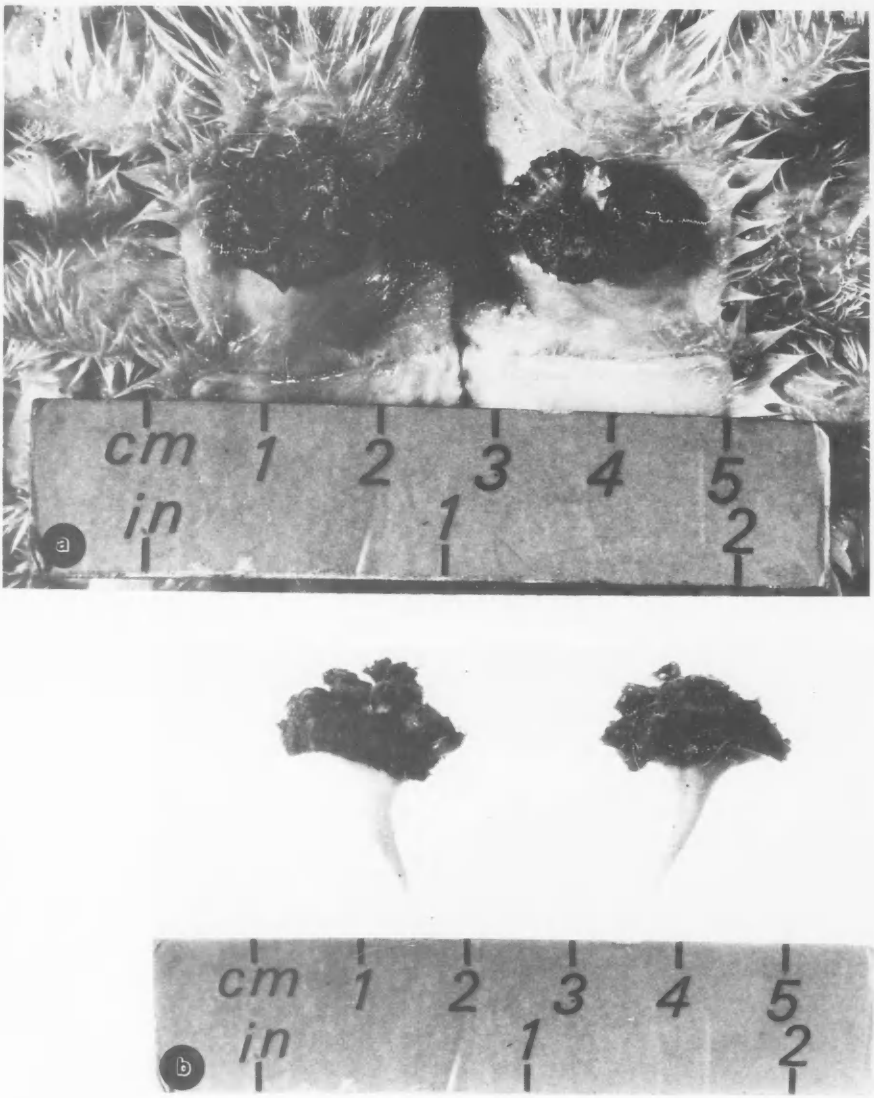


FIGURE 8.—Spermathecal plugs in formalin preserved female *Erimacrus isenbeckii*. a, ventral view of third thoracic sternite, with anterior towards the top of page, showing both gonopores with plugs; b, plugs removed from female crab; c, both pores closed (no plugs); d, both pores open. Plugs in live animals were whitish in color.

cm 1 2 3 4 5
in 1 2
d

cm 1 2 3 4 5
in 1 2
c

embryos were caught, the highest proportions occurred in February and May. Empty egg cases became proportionately more abundant from June through August. The eight ovigerous females caught ranged from 56 to 87 mm CL. Fecundity estimates for six ovigerous females ranged from 34,000 to 160,400 embryos, averaging 0.9 mm in diameter (Table 4). Uneyed embryos were orange in color, whereas eyed embryos were dark brown.

Molting and Growth

Seasonality

Molting periodicity of hair crabs in the EBS is not well understood, owing to the lack of seasonal data. Summer cruises during 1979-84 turned up only three molting male crabs. Molting and soft-shell crabs comprised only 2.2% of males (65 crabs) and 8.9% of females (22 crabs) (Table 3B). Molting females were more abundant in July samples, but males showed no particular pattern.

Molting was much more apparent during the February 1983 cruise. Thirty percent (9 of 30) of female crabs were soft shell. Among the 136 males captured, 9% (12) were soft shell and 11% (15) were undergoing ecdysis. In contrast to the 1983 results, almost no molting was observed in February 1985. All 56 males captured were new hard shell or older, and only 1 (6.7%) of 15 females was soft shell.

In the EBS, based on the percentage of crab that we classified as new hard shell each year, an average of 79% of the large males (>89 mm CL), 95% of the small males (<90 mm CL), and 84% of the females appeared to have molted by the time the summer survey occurred.

Size Range

During the period 1979-84, 3,091 specimens of *E. isenbeckii* were captured in NMFS summer surveys, of which only 248 were females (Table 5). The average size of males caught was 96.1 mm CL

TABLE 4.—Estimated egg number and condition for six ovigerous female *Erimacrus isenbeckii* caught in the eastern Bering Sea from 1979 to 1985. Hyphens indicate no data taken.

Length (mm)	Date caught	Total[1] eggs	Egg condition	Egg color	Mean diameter[2] (mm)
65	9·82	107,900	—	—	—
69	5·80	103,400	uneyed	orange	0.86
74	9·81	113,600	eyed	—	—
79	7·85	160,400	uneyed	orange	—
82	5·80	99,800	eyed	dark brown	0.94
87	5·80	33,500	uneyed	orange	0.88

[1]Estimated from total dry weight of clutch (see methods).
[2]No obvious difference between length and width.

TABLE 5.—Descriptive statistics of *Erimacrus isenbeckii* caught during NMFS surveys, 1979-84, in the eastern Bering Sea. Carapace lengths were measured from the right orbit.

	Mean	*s*	Range	Number measured
Males				
length (mm)	96.1	12.7	17-145	2,810
width (mm)	93.5	17.0	18-133	1,089
weight (g)	714.3	339.5	3-1574	703
Total males caught		2,843		
Females				
length (mm)	65.5	16.2	14-111	246
width (mm)	67.2	16.5	14-109	232
weight (g)	197.1	137.1	4-623	179
Total females caught		248		
Total caught		3,091		

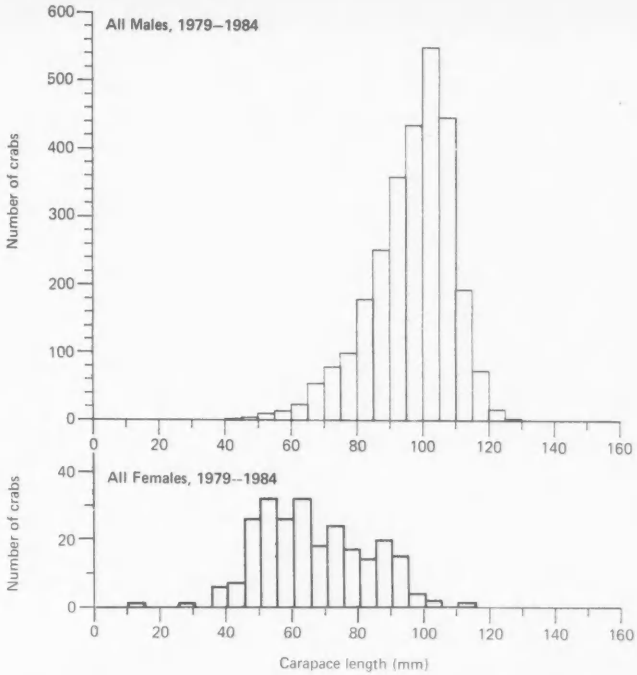


FIGURE 9.—Carapace length frequencies of *Erimacrus isenbeckii* collected during NMFS summer surveys in the eastern Bering Sea, 1979-84. Data for all 6 years were combined. Note scarcity of specimens below about 45 mm CL.

(range 17-145 mm); females averaged 65.5 mm CL (range 14-111 mm). Median values were 98 mm CL for males and 63 mm CL for females. The combined length-frequency distributions of male and female hair crab, 1979-84, are shown in Figure 9. In order to facilitate conversion between different methods of measurement, we calculated regression relationships between length, width, and weight (Table 6).

DISCUSSION

Distribution and Abundance

The decline of the EBS hair crab population occurred during the same time period (1980-84) in which substantial declines of red and blue king crabs (*Paralithodes camtschatica* and *P. platypus*, respectively), as well as two species of snow (Tan-

TABLE 6.—Regression relationships for length, weight, and width of *Erimacrus isenbeckii*, from the eastern Bering Sea. Length is carapace length from orbit.

	R^2	*n*
Males		
length (mm) = 2.28 + 0.974 width (mm)	0.945	1,087
L_n weight (g) = −7.24 + 3.02 L_n length (mm)	0.926	703
Females		
length (mm) = 1.87 + 0.938 width (mm)	0.969	231
L_n weight (g) = −6.73 + 2.86 L_n length (mm)	0.946	178

ner) crab (*Chionoecetes bairdi* and *C. opilio*) also occurred in the EBS (Stevens and MacIntosh 1985[9]). These events may be responses to common causes such as changes in the oceanographic environment of the Bering Sea, increased predation, or increased incidence of disease. A. K. Sparks[10] indicated that a presumptive viral infection was present in 13 of 20 hair crabs collected opportunistically in 1983, and in 2 of 3 examined from 1984 collections in the EBS. Although damage to the antennal gland in these infections suggest that the disease is fatal, this has not been proven. Fishery removals have ranged from <1% (before 1980) to a high of 11% (1983) of the estimated population of large males, which is probably underestimated (see Tables 1 and 2). Thus fishing pressure does not seem to have played a significant role in the population decline. A more plausible explanation of the decline in the hair crab population (and perhaps other EBS crab species as well) is that very large year classes may have been produced in the EBS in the late 1960's or early 1970's, recruited to the fisheries in the period 1977-80, and then declined to lower levels as these crabs succumbed to mortality. Historical data support this hypothesis for red king crab, and it may be applicable to hair crab as well as other species of crab.

Changes in the proportions of the hair crab population in various districts of the EBS (Table 2) may indicate that many crabs shifted from the Bristol Bay and Northern Districts into the Pribilof District and back again over the 6 survey years, or more likely, that the eastern and northern segments of the population began to decline several years before the Pribilof population, which may have been increasing until 1982. Bottom temperature did not seem to be an important factor in determining distribution of hair crab since there was no narrow range of temperature consistently associated with high catch rates.

The low percentage of female hair crab caught in the annual NMFS summer trawl surveys, compared with the relatively high percentage caught in the May 1983 survey, might be a result of gear selectivity, and possibly indicates that females were more abundant in shallow (<25 m) water or nearshore habitats that were not heavily sampled during the summer surveys. Low proportions of female hair crabs have also been captured during surveys around Hokkaido, where females comprised only 1-12% of the total catch (Kawakami 1934; Hirano 1935; Matui 1970). Hirano (1935) felt that the low numbers could be attributed to the small size of females in relation to mesh size of the net used for sampling, a preference by females for different habitats, or perhaps frequent burrowing. In a laboratory experiment, Hirano noted that females burrowed as deep as 13-15 cm for up to 4 days, whereas males burrowed for relatively short periods of time and usually so shallowly that the carapace protruded at the surface. Most (90%) of the adult females collected in the May 1983 survey were caught by trawl or try-net between the hours of 1900 and 0600. Abe (1973), however, found very little difference in the trawl catches of females between night (two 1-h tows at 2100 and 0330; 11 caught) and day (two 1-h tows at 0900 and 1500; 9 caught), although he did find that females were significantly more vulnerable to crab pots during the day (281 crabs/118 pots) than at night (46 crabs/115 pots). It is possible that increased activity of females during the day resulted in the higher pot-catch. During Abe's survey, females comprised 35% (347) of the total catch of 996 hair crab.

Depth, temperature, and substrate preferences appear to be similar for EBS and Japanese populations of hair crab, although maximum annual bottom temperatures in the EBS rarely exceed 12°C.

Compared with the distribution of juvenile and adult hair crab in the EBS, hair crab larvae were distributed primarily north and northwest of Unimak Island (Fig. 10) and concentrated in the upper 40 m of the water column, during surveys in the spring and summer of 1976-81 (Armstrong et al. fn. 4). Highest concentrations (over 5,000 larvae/100 m^2) occurred from Unimak Island north to about 55°30′N, mostly along the 50 m isobath. Low numbers (1-1,000/100 m^2) were scattered broadly over shelf and slope areas, but were more abundant along the 100 and 200 m isobaths. Sparse sampling occurred in the Pribilof Islands area during those surveys, but extensive sampling was conducted there in May 1983 (Arm-

[9]Stevens, B. G., and R. A. MacIntosh. 1985. Report to industry on the 1985 eastern Bering Sea crab survey. NWAFC Processed Rep. 85-20, 48 p. Kodiak Facility, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615.

[10] A. K. Sparks, Fisheries Research Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. May 1985.

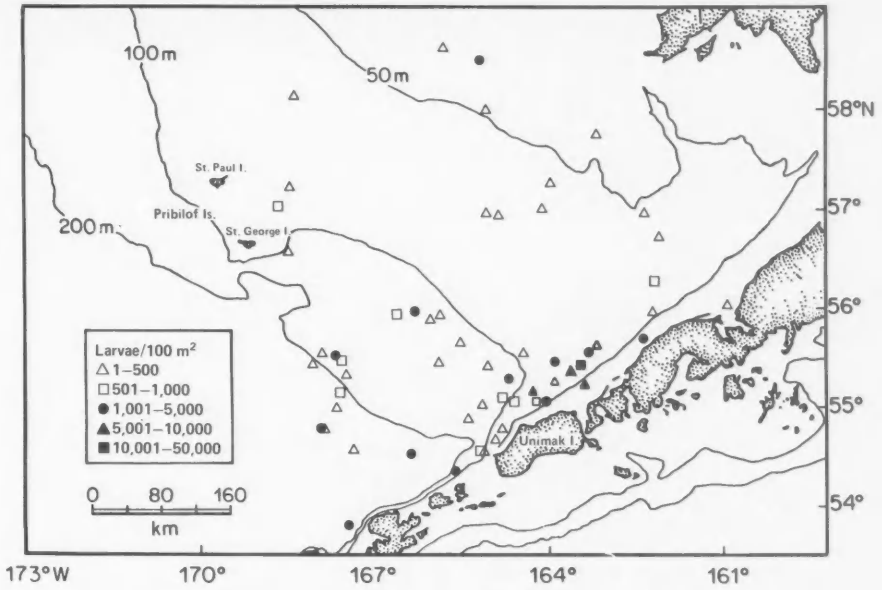


FIGURE 10.—Locations and densities of *Erimacrus isenbeckii* larvae collected in the southeastern Bering Sea, 1976-81. Locations where no larvae were found are omitted. With permission, from Armstrong et al. 1983 (see text footnote 4).

strong et al. 1984[11]). Highest concentrations (over 20,000 larvae/100 m^2 at one station) were found in waters 40-80 m deep, within about 24 km of St. Paul Island. Very few larvae were found near St. George Island.

Reproduction

The gonopore plugs found in female hair crab collected by NMFS resembled those described by Yoshida (1940) as having a "distal end that swells into an irregular form outside the aperture" and were of male origin (Morado[12]). The proximal tip of the plug extends to the spermatheca, as noted also by both Yoshida and Hirano (1935). The flexible, swollen membrane (Fig. 8c) that closed the aperture of some females is apparently not an exogenous plug, but a part of the female crab's body. The purpose of gonopore plugs is not known, but Hirano (1935) has conjectured that they serve to prevent copulation with other males during the period between the completion of copulation and spawning. They may also prevent degradation of the sperm from contact with seawater. Hartnoll (1969) reported that similar plugs have been observed in *Cancer irroratus, C. pagurus, Callinectes sapidus*, and *Carcinus maenas* and surmised that they prevent loss of sperm from female crabs which mated while still soft, or that they are a vestigial remnant of a hard sperm-case applied externally by more primitive ancestral brachyurans.

The following sequence of events is suggested by the observed associations between shell condition of female crabs and the presence or absence of gonopore plugs. After mating, the plugs loosen and slough off, either by mechanical abrasion (Yoshida 1940) or by dissolution from within as

[11]Armstrong, D. A., J. L. Armstrong, G. Jensen, R. Palacios, and G. Williams. 1984. Distribution, abundance, and biology of blue king and Korean hair crabs around the Pribilof Islands. Interim Rep. OCSEAP/OMPA contract No. 83-ABC-00066. Office of Marine Pollution Assessment, Alaska Office RD/MPF24, P.O. Box 1808, Juneau, AK 99802.

[12]J. F. Morado, Fisheries Research Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. May 1982.

the female's ovaries mature (Hirano 1935), leaving the swollen membrane in place. The membrane eventually becomes flaccid, perhaps to allow egg extrusion. As the spawning period approaches, the spermatophores gradually break up and release spermatozoa. Fertilization occurs, either as the eggs are extruded (Kawakami 1934; Yoshida 1940) or afterwards, perhaps by contraction of the sperm sac and expulsion of the spermatozoa over the eggs (Sakurai et al. 1972). Our estimates of the number of external embryos carried by EBS hair crabs are in accordance with Sakurai et al. (1972, see Literature Review).

Molting and Growth

Molting frequency varies with age and sex of the crab. Because the percentage of recently molted male crabs declined with increasing size, the NMFS data appears to support Yamamoto (1971), who indicated that molting frequency of males decreases as size increases. Yoshida (1941) claimed that female hair crab molt every other year. Our data neither support nor refute this. However, old and new shell conditions are difficult to distinguish in hair crab, because shell discolorations and epibiota are uncommon. Thus, it is difficult to determine when a particular crab last molted. A higher frequency of molting in February (based on the 1983 data, Table 3B) for EBS hair crab tends to support the conclusions of Abe (1984[13]) and Sakurai et al.(1972) (Fig. 3) that hair crab molt and mate in winter, although the 1985 data did not. The second period of molting exhibited by female crabs in July tends to support the contention by Sakurai et al. that multiparous females molt and breed from August to November; however, females exhibited a low frequency of molting in August. Crabs of all sizes molted in both periods.

The effect of temperature on molting periodicity of hair crab is unknown. Mean bottom temperatures that were 2.5°C warmer in February 1985 than February 1983 for stations sampled for hair crab in both those years could have affected the onset of molting in 1985. Whereas in 1983, 22% of the hair crab caught were molting or in soft-shell condition, in 1985 only 1% were.

Abe (1982) determined the mean carapace length of 14 male and 13 female hair crab postlarval instars (Table 7) through length-frequency analysis of 10,547 individuals. For the first 9 instars, there was no difference in mean carapace length between males and females. However, after sexual maturity (i.e., sizes greater than about 55 mm RL or 50 mm CL) females showed less growth per molt than males, although growth increments decreased with age for both sexes. Abe plotted postmolt carapace lengths (L_{n+1})

[13]Abe, K. 1984. Reproductive cycle of hair crab. Unpubl. manuscr. Chief, Fisheries Resources Division, Hokkaido Wakkanai Fisheries Experimental Station, 5-4 Horai, 4-chome, Wakkanai, Hokkaido, 097, Japan. Presented at the hair crab conference, Yoichicho, Japan, January 31, 1984.

TABLE 7.—Mean carapace length (mm RL) for each postlarval instar of male and female hair crab, *Erimacrus isenbeckii*, (from Abe 1982), and calculated mean growth increment for the next molt.

Instar number	Mean length[1] (mm)		Percent increase		Calculated Orbit length (male)
	male	female	male	female	
C1	5.2		35		
C2	7.0		24		
C3	8.7		44		
C4	12.5		25		
C5	15.6		31		
C6	20.4		34		
C7	27.4		22		
C8	33.5		38		
C9	46.4		27	20	41.9
C10	59.1	55.9	24	18	53.6
C11	73.3	65.8	20	13	66.7
C12	88.2	74.1	17	13	80.4
C13	103.5	84.0	14		94.5
C14	117.5				107.4

[1]Lengths of females were same as males for instars 1-9.

against premolt carapace lengths (L_n) and derived the following equations (not converted to CL):

Both sexes (<50 mm RL)	$L_{n+1} = -0.40 + 1.336\ (L_n)$
Males (>50 mm RL)	$L_{n+1} = 11.68 + 1.036\ (L_n)$
Females (>50 mm RL)	$L_{n+1} = 9.49 + 0.998\ (L_n)$

Abe (1982) plotted the regression of percent growth per molt on length, and estimated maximum lengths to be 125 mm RL (116 mm CL) for females and 177 mm RL (162 mm CL) for males. The largest hair crabs observed by NMFS in the EBS (Table 5) were smaller than these projections, as were those caught near Hokkaido by Abe (1982), who reported maximum lengths of 152 mm RL (139 mm CL) for males and 105 mm RL (97 mm CL) for females. Reportedly, female hair crabs from Hokkaido rarely reach a carapace length >80 mm RL (73 mm CL) (Sakurai et al. 1972). In contrast, over 20% of the females caught in the EBS were >80 mm CL. However, NMFS trawl gear caught few hair crab <40-50 mm CL, and juvenile and female crabs may occupy rocky nearshore habitat which cannot be adequately sampled by such gear.

The mean age of hair crab in the fishable population can be estimated from available data. Abe (1982) concluded that male crabs mature in their 10th postlarval instar, about 33 months after hatching, at about 60 mm RL (54 mm CL; Fig. 3). According to Yamamoto (1971), they would require one more annual molt to reach stage C11 in their fourth year. At this size, crabs may molt annually or biennially. Male crabs landed in the EBS fishery averaged 106 mm CL (116 mm RL) in 1984, or about stage C14 (Tables 1, 7). To attain this size would require 3 molts from C11, and these crabs would range in age from 7 to 10 years depending upon whether their last 3 molts were annual or biennial. If any failed to molt more than 1 year in a row, they would be age 11 at this size. Abe (fn. 13) (Fig. 3) indicated that male hair crab in Hokkaido waters reach similar sizes at the age of 6 years (assuming none skip molted).

Resource Potential and Management

Because of the great declines in abundance of the Bering Sea populations of *E. isenbeckii* from 1979 to 1984, this fishery will probably not be of great economic importance in the near future. If abundance increases in the future and prices remain adequate, this fishery might become lucrative, albeit on a small scale relative to other Bering Sea crab fisheries. The species could then probably support a small boat fishery in the Pribilof Islands. Hair crab are still in high demand in Japan.

The EBS hair crab fishery is not intensively managed. Fishing may occur year-round and is not limited by quotas. However, only males may be landed and gear is restricted to crab pots. There is no minimum size limit since the marketable size is large relative to the probable size of male maturity (about 54 mm CL), although the latter has not been adequately determined.

As a result of distribution and habitat differences as well as gear selectivity, the size-frequency distributions of NMFS collections have been largely unimodal with few juveniles and females in the catch. Thus, a thorough study of EBS hair crab reproduction and recruitment has not been feasible. Much useful information could probably be gained by systematic, year-round sampling of rocky heterogeneous habitats around the Pribilof Islands with appropriate gear such as rock dredges and beam trawls. Some data of this sort have already been collected by Armstrong et al. (fn. 11) and during other NMFS surveys, but are too limited to allow an improved understanding of growth rates, or the seasonality of molting and spawning of hair crab in the EBS. Further information on maturity, growth, and mortality is critical for informed management and will be necessary if this fishery gains importance.

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EXPLORATION FOR GOLDEN CRAB, *GERYON FENNERI*, IN THE SOUTH ATLANTIC BIGHT: DISTRIBUTION, POPULATION STRUCTURE, AND GEAR ASSESSMENT[1]

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ABSTRACT

Exploratory trapping for golden crab, *Geryon fenneri*, was conducted from 5 August 1985 to 21 February 1986 off South Carolina and Georgia. A buoyed system with strings of six traps (three side-entry Fathoms Plus and three top-entry Florida traps) was fished in six depth strata: 274-366 m, 367-457 m, 458-549 m, 550-640 m, 641-732 m, and 733-823 m. A total of 3,152 *G. fenneri* (2,661.9 kg) were collected at sampled depths between 296 and 810 m. The only other numerically important species caught was the jonah crab, *Cancer borealis* (864 individuals, 227.5 kg).

Catches of golden crab were highly variable between strata. Catch per trap increased from 1.6 crabs (1.67 kg) in the shallowest stratum sampled to a maximum abundance of 22.3 crabs/trap (18.04 kg/trap) in the 458-549 m depth zone. Catches abruptly declined in the deeper strata sampled.

Number of golden crab per trap (1.7:1) and weight per trap (1.6:1) in the Florida trap exceeded that in the Fathoms Plus trap for all completed sets. Traps yielded golden crab as small as 85 mm CW but the greatest proportion of crabs was >100 mm CW. Over 90% of all individuals exceeded 114 mm CW which is the minimum size of red crab, *G. quinquedens*, accepted for commercial utilization. Male golden crab were more numerous and larger than females.

Crabs of the genus *Geryon* (Brachyura: Geryonidae) are deepwater inhabitants of the Atlantic, Indian, and Pacific Oceans (Rathbun 1937; Monod 1956; Christiansen 1969; Manning and Holthuis 1981). Species reported off the United States in the western Atlantic and Gulf of Mexico include the red crab, *G. quinquedens* Smith, and the golden crab, *G. fenneri* Manning and Holthuis. At the time *G. fenneri* was described (Manning and Holthuis 1984), its geographic and bathymetric distribution included the continental slope off eastern Florida, the Florida Straits, and the Gulf of Mexico. An exploratory fishing effort in 1984 collected the first known specimens of golden crab off South Carolina[4], and it is now known that golden crab occur in waters off Bermuda (Luckhurst in press).

Both *G. quinquedens* and *G. fenneri* have been the target of limited and sporadic commercial fishing efforts off the east coast of the United States (Gerrior 1981), in the Gulf of Mexico. (Otwell et al. 1984; National Marine Fisheries Service 1986[5]), and off Bermuda (Luckhurst in press). Although much information is available concerning the biology and commercial fishery of red crab (summarized by Gerrior 1981), biological information on golden crab is more limited. Otwell et al. (1984) demonstrated exploratory trapping and processing techniques for golden crab from the Gulf of Mexico.

The initiation of a small commercial crabbing enterprise during 1984 in South Carolina yielded promising quantities of golden crab[6]. We began the present study to determine the fishery potential, compare trap designs, delineate bathymetric distribution, and describe the biology of golden crab in the South Atlantic Bight. This report documents results on catch rates, size and sex compo-

[1]Contribution No. 232, South Carolina Marine Resources Center, Marine Resources Research Institute.

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[4]South Carolina Wildlife and Marine Resources Department, unpubl. data, courtesy Charles Wenner, Marine Resources Research Institute, Charleston, SC.

[5]National Marine Fisheries Service. 1986. Species profile: deep red crab, *Geryon quinquedens*, Smith and golden crab, *Geryon fenneri*, Manning and Holthius, 1984 from the southeastern U.S. south of Cape Hatteras, N.C. U.S. Dep. Commer. Natl. Mar. Fish. Serv., NOAA, Pascagoula Lab., Latent Resour. Rep., 17 p.

[6]H. Holley, commercial fisherman, Charleston, SC, pers. commun. 1985.

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sition of *G. fenneri* as a function of depth and trap type, and examines aspects of adult life history and reproductive biology of this species in the South Atlantic Bight.

METHODS

Cruises were made during the period from 20 June 1985 to 21 February 1986 on board the South Carolina Wildlife and Marine Resources Department (SCWMRD) research vessels *Oregon* and *Lady Lisa*, and the NOAA ship *Chapman*. All vessels were equipped with large capacity hydraulic systems and a heavy duty pot hauler.

Two commercially available trap designs were used to sample crabs. The Fathoms Plus[7] traps are oval (85 cm long × 66 cm wide × 30 cm high) and constructed of injection molded plastic. The trap has two side-entry funnels that can be enlarged by removing more of the plastic funnel's inner lip. The original, oval funnel opening is 10 cm × 20 cm. Both funnels were cut out to a maximum opening size of 14 cm × 22 cm. Traps were weighted with chain, making the total weight of each trap 11 kg. The Florida trap is an injection molded, high-impact plastic version of a Florida spiny lobster trap (82 cm long × 61 cm wide × 45 cm high). The top of the trap is constructed of wood lathing to provide a biodegradable escape panel. The top entrance funnel has adjustable panels and is 20 cm × 25 cm in the most open position, as fished throughout the study. Two strips of poured concrete in each end of the trap provided ballast, making the total weight of the trap about 22.7 kg.

Traps were baited with 1.2-1.6 kg of clupeids. Three Florida and three Fathoms Plus traps were alternately attached at 61 m intervals to 365.6 m of groundline. The groundline was constructed of 8 mm diameter Iceline, a dacron, polyethylene line that has a high tensile strength relative to its diameter. A small weight consisting of ~9.0 kg of chain was attached to one end of the groundline and an anchor (~25 kg) was attached to the buoyline end of the gear. Buoy lines were 366 m sections of 8 mm Iceline joined together to achieve at least a 2:1 ratio of line to water depth. Four inflatable net buoys and a spar buoy with radar reflector were attached to the buoyline.

Six depth strata were sampled between lat. 29°53.1′-32°20.0′N and long. 78°01.5′-79°24.8′W: 274-366 m (stratum 1), 367-457 m (stratum 2), 458-549 m (stratum 3), 550-640 m (stratum 4), 641-732 m (stratum 5), and 733-823 m (stratum 6). Three sets of six traps each were made approximately 1-2 km apart within a depth stratum over a 24-h period. Sampling locations for each set were selected by making fathometer transects of the potential fishing area to determine depth and bottom type. Because of bad weather and logistical constraints all strata did not receive equal effort (Table 1).

The first trap type on the groundline was randomly selected with trap type alternating until six traps (three of each type) were attached. The exception to this arrangement occurred in the deepest stratum (733-823 m) where only the Fathoms Plus trap was used.

Fishing duration was standardized at 20 hours; however, poor weather conditions and logistical considerations altered this. Average fishing duration within strata exceeded 17 hours (Table 1).

Bottom temperature was determined in each depth stratum by reversing thermometers. Bottom sediments were sampled by a geological rocket grab for each group of three sets made in an area. Sediments retrieved were frozen on board and examined under a microscope for gross characterization in the laboratory. Sampling depth and location were recorded at deployment of the anchor.

Decapod crustaceans in each trap were identified, counted, and weighed. Catches from damaged traps or those sets that moved due to currents were excluded from analyses of distribution and abundance, but were included in biological studies of size and sex composition. Each golden crab was individually sexed, measured to the nearest millimeter (carapace width, CW, distance between the tips of the fifth lateral spines; carapace length, CL, distance from the diastema be-

TABLE 1.—Mean, standard deviation, minimum, and maximum fishing duration of trap sets, for *Geryon fenneri*, within six strata sampled from August 1985 to March 1986.

Stratum	No. sets	Fishing duration (h)			
		$\bar{y}$	(*s*)	Min.	Max.
1	8	17.5	3.75	12.4	21.2
2	32	18.8	2.36	14.0	23.2
3	16	20.5	2.07	16.2	23.7
4	6	22.9	1.15	21.5	24.7
5	4	17.2	0.73	16.4	18.1
6	4	20.2	5.69	11.7	23.3

[7]Reference to trade names does not inply endorsement by the National Marine Fisheries Service, NOAA.

tween the rostral teeth to the posterior edge of the carapace, along the midline), and most were weighed to the nearest gram. The number of missing chelae and pereopods was recorded for each crab, as was molt condition and presence of chitinolysis and poecilasmatid barnacles, *Trilasmis inaequilaterale*, on the exoskeleton. Molt condition of *G. fenneri* was modified from criteria established by Beyers and Wilke (1980) for *G. quinquedens* (probably *G. maritae* Manning and Holthius) and consisted of five categories:

1) Hard - carapace at maximum strength, fouling by barnacles or chitinolytic bacteria minimal,
2) Hard old - carapace strong but heavily fouled by barnacles and abraded or blackened by chitinolytic bacteria,
3) Soft old - resorptive line along posterolateral sides of the carapace is weak; carapace heavily fouled as with hard-old condition,
4) Soft new - carapace soft or jellylike with no fouling, and
5) Hard new - carapace cracks under pressure and is not fouled.

Female *G. fenneri* were examined for evidence of egg extrusion and mating. Presence of eggs or egg remnants on pleopods and the size, shape, and physical condition of vulvae, as described by Haefner (1977), were noted. We examined seminal receptacles for presence of sperm or spermatophores and for relative size.

Ovaries from 72 of the 166 female *G. fenneri* captured were initially classified by relative size and color following the scheme described by Haefner (1977) for *G. quinquedens*. After gross classification of ovaries, tissues were removed for histological preparation and examination in order to describe ovarian structure and validate assigned ovarian stages. Tissues were fixed for at least 48 hours in 10% seawater formalin. After fixation, tissues were dehydrated, cleared, and embedded in paraffin. Sections were cut at 6-9 μm and were stained with Gill's hematoxylin and counterstained with eosin-Y. Oocytes from *G. fenneri* were measured using an ocular micrometer.

Testes and vas deferentia from three *G. fenneri* were fixed for 24 hours in 2.5% glutaraldehyde, rinsed in cacodylate buffer, and dehydrated in ethanol. Tissues were then critical-point dried, sputter coated, and examined using a Jeol JSM-35C scanning electron microscope (SEM).

RESULTS

Distribution and Relative Abundance

The 70 valid sets (416 individual trap observations) caught 3,152 *G. fenneri* (2,661.9 kg) at sampled depths between 296 and 810 m. The only other numerically important species caught was the jonah crab, *Cancer borealis* (864 individuals, 227.5 kg).

Catch per trap increased from 1.6 crabs (1.67 kg) in the shallowest stratum to a maximum abundance of 22.3 crabs/trap (18.04 kg/trap) in the 458-549 m depth zone (Fig. 1). Catches then abruptly declined with increasing depth. The absence of golden crabs in traps fished between 550 and 640 m appears to be related to unsuitable

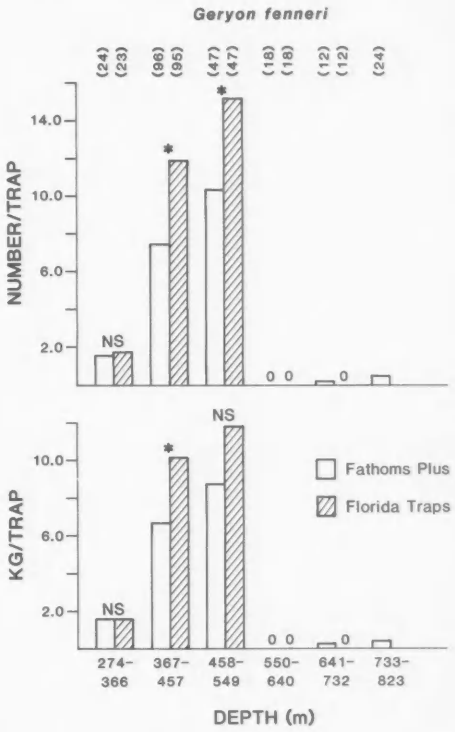

FIGURE 1.—Catch per trap of *Geryon fenneri* for six depth strata sampled. Effort (number of traps) is shown in parentheses. Statistical significance of catches between trap types, as determined by two sample t-test, is indicated by * ($P < 0.05$). NS indicates no significant difference in catch rates between the two trap types.

sediments at sites in this stratum since grab samples contained coral fragments and rubble. At shoaler locations where golden crabs were abundant, sediments were a mixture of soft silt-clay, molluscan shell fragments, and foraminiferan tests. Temperatures at sites where golden crabs were collected ranged from 7.14° to 9.15°C.

The number of golden crab per trap (11.4) and the weight of golden crab per trap (9.37 kg) in the Florida trap exceeded that in the Fathoms Plus trap (7.0 individuals, 6.16 kg) for all combined sets (Table 2). Statistical results by strata using the two-sample t-test or an approximate t-test when variances were heterogeneous (Sokal and Rohlf 1983), indicated significantly more crabs were collected with the Florida trap than with the Fathoms Plus trap from 367 to 457 m (stratum 2) and from 458 to 549 m (stratum 3) (Fig. 1, Table 2). Weight per trap was significantly different for the 367-457 m stratum only.

Size and Sex Composition

Male *G. fenneri* were significantly more numerous than females, outnumbering them by ~18:1. No ovigerous females were collected during the sampling period. Dominance of males was statistically significant for strata 1-3 (Table 3). In these depth strata, males were 20 times as numerous as females. In depths of 550-732 m, a male was the only crab collected. In the deepest stratum sampled (733-823 m), females significantly outnumbered males 2.9:1. Although the Florida trap caught significantly more crabs than the Fathoms Plus trap overall, no significant difference was noted in the number of female crabs between those two trap types (χ^2 test, $P > 0.5$).

The 3,217 golden crabs which were measured ranged from 85 to 193 mm in carapace width and weighed from 100 to 2,109 g. Average weight of male golden crab collected during the study was 927 g ($s = 373.448$, $n = 1{,}640$) while average weight of females was 443 g ($s = 289.385$, $n = 86$). Carapace width-frequency distribution for *G. fenneri* gave modes at 155 mm for males and 100 mm for females (Fig. 2). The largest crab collected measured 193 mm and weighed 2,091 g.

Linear least-squares and functional regression equations (Ricker 1973; Sokal and Rohlf 1983) relating carapace length and live wet body weight with width are in Table 4. Width-weight relationships were calculated from data on individuals that were not missing appendages.

Of the 3,183 golden crabs examined for missing appendages, 2.4% were missing one or both chelae. Pereopods were missing from 307 individuals (9.6%).

Examination of carapace width and weight statistics for each depth stratum showed that mean size of male *G. fenneri* was greatest for the shallowest (274-366 m) and deepest (733-823 m) strata sampled (Table 5). For females, however, mean carapace width and weight were greatest in the deepest zone. At depths of peak abundance, mean carapace width ($t_s = 4.70$, $P < 0.001$) and mean body weight ($t_s = 2.70$, $P < 0.01$) of male crabs were significantly greater in the 367-457 m than in the 458-549 m depth stratum. No signifi-

TABLE 2.—Results of t-test (T_s) comparisons of mean number and weight (kg) per trap for two trap types (FM+ and FLA) fished in each depth stratum for *Geryon fenneri*. Standard deviation is noted in parentheses; * indicates significance at 0.05 level.

	Number/trap			Weight/trap		
Stratum	FM+	FLA	T_s	FM+	FLA	T_s
1	1.6(1.92)	1.8(2.21)	0.14	1.66(1.912)	1.80(2.157)	0.14
2	7.5(5.96)	11.9(9.95)	2.16*	6.67(5.097)	10.02(7.651)	2.06*
3	10.4(5.08)	15.2(7.08)	2.22*	8.82(4.164)	11.84(4.752)	1.91
4	0	0	—	0	0	—
5	0.1	0	—	0.07	0	—
6	0.5(0.28)	—	—	0.43(0.321)	—	—
Total	7.0(5.98)	11.4(9.38)	8.51*	6.16(5.052)	9.37(7.078)	6.18*

TABLE 3.—Frequency of male and female *Geryon fenneri* within each depth stratum. Asterisks denote significant deviation ($P < 0.05$) from 1:1 by Chi-square analysis.

	Strata (m)					
Sex	274-366	367-457	458-549	550-640	641-732	733-823
Male	84*	1,790*	1,165*	0	1	11
Female	3	91	41	0	0	32*

cant differences, however, were noted in mean carapace width ($t_s = 0.85$, $P > 0.05$) and mean body weight ($t_s = 1.48$, $P > 0.05$) of females from these same strata.

Of the two traps used, the Fathoms Plus trap caught larger and heavier golden crabs than did the Florida trap. Mean carapace width ($\bar{y} = 143$ mm, $s = 19.69$, $n = 1303$) of crabs in the Fathoms Plus trap was significantly larger than that of crabs in the Florida trap ($\bar{y} = 139$, $s = 20.21$, $n = 1914$) [$t_s = 5.478$, $P < 0.001$]. A statistically significant difference was also noted for mean weight (Fathoms Plus: $\bar{y} = 928$, $s = 366.77$, $n = 775$; Florida: $\bar{y} = 881$, $s = 377.69$, $n = 951$) [$t_s = 2.598$, $P < 0.001$].

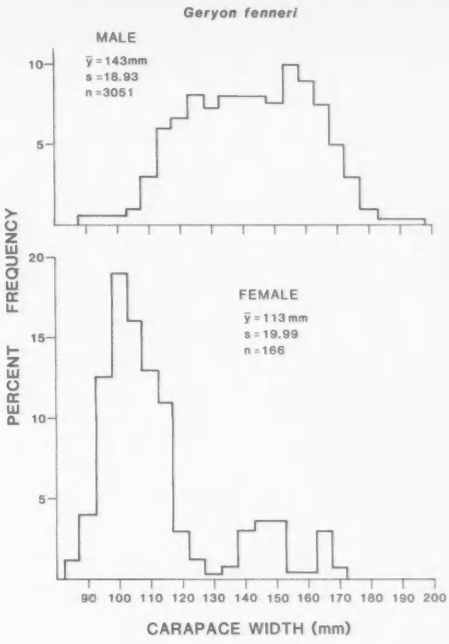

FIGURE 2.—Width-frequency distributions of male and female *Geryon fenneri* caught in traps. $\bar{y}$ = mean; s = standard deviation; n = number of individuals.

TABLE 4.—Least-square linear and geometric mean functional regression equations of carapace length (CL) and live body weight (WT) on carapace width (CW) for each sex of *Geryon fenneri*. Length and width units are millimeters while weight units are kilograms. All least square regressions were significant at $\alpha = 0.05$.

Sex	Least squares equation	n	r^2	GM functional equation
Male	CL = −9.5 + 0.9 CW	3,042	0.95	CL = −11.9 + 0.9 CW
	$\log_{10}$ WT = −4.74 + 3.54 ($\log_{10}$ CW)	1,453	0.94	$\log_{10}$ WT = −4.99 + 3.66 ($\log_{10}$ CW)
Female	CL = 4.0 + 0.8 CW	141	0.92	CL = 0.7 + 0.8 CW
	$\log_{10}$ WT = −3.97 + 3.14 ($\log_{10}$ CW)	74	0.91	$\log_{10}$ WT = −4.27 + 3.29 ($\log_{10}$ CW)

TABLE 5.—Size and weight statistics of male and female *Geryon fenneri* from sampled depth strata. $\bar{y}$ = mean; s = standard deviation, n = number of individuals.

Sex	Stratum (m)	Carapace width (mm) $\bar{y}$	Min.	Max.	s	n	Weight (g) $\bar{y}$	s	n
Male	274-366	156	117	186	14.4	84	1,064	339.15	84
	367-457	144	100	190	18.1	1,790	937	354.03	983
	458-549	140	88	193	19.9	1,165	884	373.47	561
	550-640	—	—	—	—	—	—	—	—
	641-732	139	—	—	—	1	809	—	1
	733-823	161	135	181	11.7	11	1,112	225.22	11
Female	274-366	105	92	113	11.2	3	189	80.88	3
	367-457	105	85	145	8.6	91	265	103.13	35
	458-549	104	85	137	9.7	41	228	70.06	16
	550-640	—	—	—	—	—	—	—	—
	641-732	—	—	—	—	—	—	—	—
	733-823	149	117	170	13.6	31	768	201.09	32

Reproductive Biology

We obtained satisfactory histological sections from 39 of 72 female golden crabs examined. From histological and gross examination we described four ovarian developmental stages: 1) early, 2) intermediate, 3) advanced, and 4) mature.

In the early stage of development, the slightly lobate ovary is very small, transparent to white in color, and bounded by fibrous connective tissue. Oocyte diameter ranged from 58 to 92 μm with a mean of 75 μm (Fig. 3A). Nuclei and nucleoli are readily apparent in the early oocytes, as are follicle or accessory cells which surround each

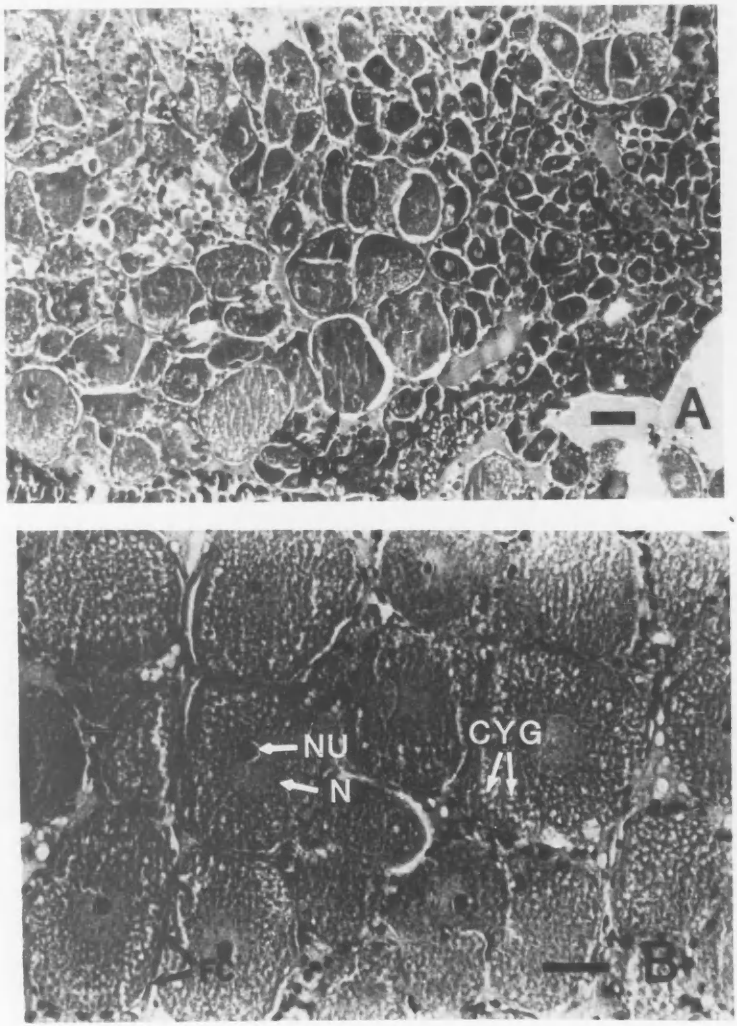

FIGURE 3.—Ovarian and testicular tissue of *Geryon fenneri*.

A. Ovarian tissue showing early (EOC) to intermediate oocyte (IOC) development. Oocytes range in size from 30 to 100 μm. Scale bar 60 μm.

B. Oocytes at the intermediate stage of development. Nucleus (N), nucleolus (NU), cytoplasmic yolk globules (CYG), follicle cells (FC). Oocyte size extremes are 100-125 μm. Scale bar 50 μm.

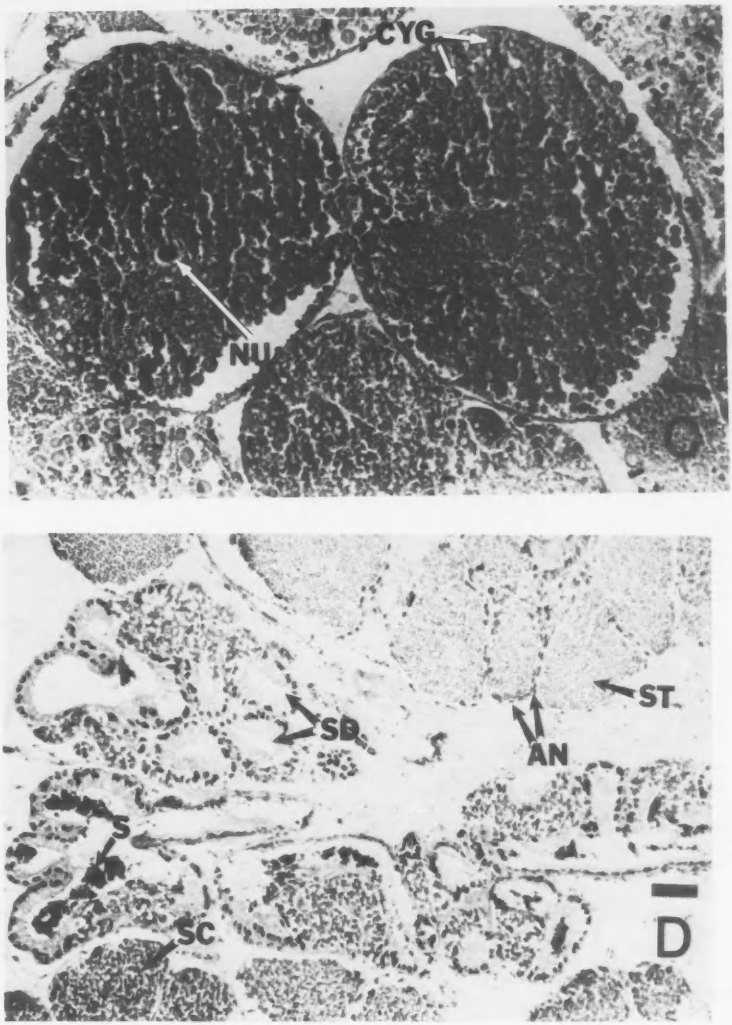

FIGURE 3.—*Continued.*

C. Oocytes in the advanced stage of development. Nucleolus (NU), cytoplasmic yolk granules (CYG). Oocytes 200-300 μm in size. Scale bar 30 μm.

D. A portion of a mature testis showing the seminiferous duct (SD) and testicular lobes containing spermatocytes (SC), spermatids (ST) and sperm (S). Accessory cell nuclei (AN). Scale bar 100 μm.

cell. In the larger oocytes, cytoplasmic vitellin globules indicative of vitellogenesis are present.

The intermediate stage ovary is yellow in color, has more pronounced lobation, and is larger than the early stage ovary. The diameter of oocytes ranged from 112 to 175 μm with a mean diameter of 145 μm. Most oocytes were undergoing vitellogenesis in this stage (Fig. 3B).

As the ovary matures to the advanced stage, the ovarian lobes become enlarged and the color becomes light orange to orange-red in color. The anterior portion of the ovary obscures the anterior hepatopancreas from dorsal view. Oocytes were 175-300 μm in diameter ($\bar{y}$ = 240 μm) and enlarge as vitellogenesis continues (Fig. 3C).

The mature ovary, brown to purple in color, is the dominant visible organ and obscures the hepatopancreas in dorsal view. Oocytes are filled with yolk globules and average 300-400 μm in diameter as vitellogenesis nears completion.

Size at sexual maturity was difficult to assess because of the small number of females collected. Overlap existed in the size of female *G. fenneri* in each stage of development.The carapace width of females in early ovarian development ranged from 85 to 116 mm ($\bar{y}$ = 104 mm, n = 27). Intermediate ovaries were present in females measuring 105-169 mm CW ($\bar{y}$ = 127 mm, n = 13) while advanced ovaries occurred at sizes from 110 to 136 mm CW ($\bar{y}$ = 123, n = 2). The 30 females with mature ovaries ranged from 97 to 169 mm CW ($\bar{y}$ = 141).

Five vulval forms were identified among the 142 females examined. Most of the females had immature vulvae (types a and b) suggesting that these crabs had not mated. The observed ovarian condition in a subsample (n = 26) of these females indicated that all had ovaries in an early stage of development (Table 6). Only one female (111 mm CW) with immature vulvae contained sperm in the seminal receptacles, indicating copulation had occurred. Type c vulvae were noted on two females, one with ovaries in early development and lacking sperm in the seminal receptacles while the other crab had mature ovaries and sperm present. Type e and f vulvae were found on the largest females collected, all of which had at least intermediate stage ovaries. Eight of the fourteen females with these vulval types whose seminal receptacles were examined had been inseminated.

Three male *G. fenneri* examined exhibited typical brachyuran reproductive morphology. The testes, which are dorsal to the hepatopancreas, were tubular and highly lobate. The testicular lobes, adjacent to the central seminiferous duct, contained spermatocytes, spermatids, and spermatozoa, suggestive of asynchronous development (Fig. 3D). In mature individuals, ripened spermatozoa were found in the seminiferous duct. Examination of the testes and vas deferentia by SEM revealed germ cells at various stages of development. Spermatids (Fig. 4A), surrounded by supportive tissue, were composed of a central nucleus framed in cytoplasm. With spermiogenesis, multiple projections or spikes form which are characteristic of developed sperm (Fig. 4A). Another portion of the same testis yielded a more advanced germ cell displaying well-defined cytoplasmic spikes (Fig. 4B). A sagittal section through the vas deferens revealed stellate spermatozoa (Fig. 4C), which had previously been embedded in this complex of supportive tissue (Fig. 4D).

TABLE 6.—Incidence of vulval type (after Haefner 1977) in relation to carapace width and gonadal condition of female *Geryon fenneri*. n = number of individuals examined.

Type	n	Carapace width (mm)	n	Gonadal condition
a	112	85-119	22	early
b	4	98-116	4	early
c	2	97-109	1	early
			1	mature
d	0	—	0	—
e	19	105-156	8	intermediate
			1	advanced
			9	mature
f	5	124-169	2	intermediate
			3	mature

Molt Condition and Fouling

Most (80%) of the 3,183 male and female *G. fenneri* were in the intermolt stage. Less than 1% of the 3,041 male golden crab showed evidence of having recently molted. The incidence of imminent or recently molted female golden crab was higher than that observed for males, with four individuals classified as premolt (soft-old) and two in the newly molted (soft-new) condition.

Most (95%) of the 3,183 *G. fenneri* examined for molt condition had blackened abraded areas on the exoskeleton, indicative of damage by chitinolytic bacteria. Exoskeleton damage was most prevalent on individuals in the intermolt (75%) and premolt (19%) condition.

DISCUSSION

Although the results of this study suggest that *G. fenneri* has a wide bathymetric occurrence in the South Atlantic Bight, the depth extremes for the species probably extend beyond those encompassed by our sampling design. Records of *Geryon* sp. and *G. affinis* (which were probably *G. fenneri*) from the Gulf of Mexico indicate a depth distribution of 365-1,455 m (Pequegnat 1970), while Luckhurst (in press) reported golden crabs from 786 to 1,462 m near Bermuda.

Although a broad bathymetric range for the species is likely, maximum abundance occurs between 367 and 549 m in our study area. This depth range coincides with that reported by Stone and Bailey (1980) for maximum trap catches of *G. quinquedens* along the Scotian Shelf and approximates the limits (320-530 m) determined by Wigley et al. (1975) by trawl and photographic methods to be most productive for that species off the northeastern United States.

Information on sediment composition taken coincidentally with fishing activities suggests that abundance of both *G. fenneri* and *G. quinquedens* is influenced by sediment type at these optimum depths. Our catches were highest on substrates containing a mixture of silt-clay and foraminiferan shell. In contrast, no golden crab were collected on rock and coral rubble bottom such as was encountered in the 550-640 m stratum. Other studies have described an association of *G. quinquedens* with soft substrates. Wigley et al. (1975) noted that bottom sediments throughout the area surveyed for red crab from offshore Maryland to Corsair Canyon (Georges Bank) consisted of a soft, olive-green, silt-clay mixture. If golden crabs preferentially inhabit soft substrates, then their zone of maximum abundance may be limited within the South Atlantic Bight. Surveys by Bullis and Rathjen (1959) indicated that green mud occurred consistently at 270-450 m between St. Augustine and Cape Canaveral, FL (30°N and 28°N). This same depth range from Savannah, GA to St. Augustine was generally characterized by Bullis and Rathjen (1959) as extremely irregular bottom with some smooth limestone or "slab" rock present. Our study indicates, however, that the bottom due east between Savannah and St. Catherines Island, GA at 270-540 m consists of mud and biogenic ooze. Further north from Cape Fear, NC to Savannah, bottom topography between 270 and 450 m is highly variable with rocky outcrops, sand and mud ooze present (Low and Ulrich 1983). Additional information on sediment type during future fishing efforts will be necessary before any validation of sediment preference by golden crab can be made.

The catch data for golden crab in our survey compares favorably with catch rates reported by Otwell et al. (1984) in the Gulf of Mexico. Although their study was not intended to assess the resource, they reported mean catch per trap values of 7.4-8.4 for the nested design fished between 210 and 340 fathoms. Information on catch rates of red crab from trap surveys and the fishery is perhaps more relevant to our study. Ganz and Herrmann (1975) reported an overall unculled mean catch per pot of 40-93 red crabs off southern New England; their study used four types of double parlor offshore lobster pots. An average catch of 26.8 red crabs per trap (conical-top entry) was reported in 360-540 m depths on the Scotian Shelf by Stone and Bailey (1980). The only available information on weight per trap was provided by Gerrior (1981) who found seasonal catch rates that ranged from a low of 8.4 kg in March to a high of 11.1 kg per pot in June. Although comparison of catch per unit of effort between these studies is questionable because trap type and fishing duration, as well as physical features of the sampling areas differ, catch per trap of golden crab in depths of maximum abundance off South Carolina and Georgia appears promising.

Comparison of catches (no./trap) between the Fathoms Plus trap and the Florida trap clearly indicate superiority of the latter for golden crab. These two traps also differed in the size and weight of individuals caught, with larger and heavier golden crab occurring in the Fathoms Plus trap. Advantages of the Fathoms Plus traps for commercial fishing operations would include their lighter weight, ease of handling, and stackable configuration which conserves deck space. Differences observed between traps may be related to trap design which affects success of entry and maximum catch (Miller 1980) or behavioral interactions which affect probability of capture (Richards et al. 1983). Although no studies have been done to evaluate behavior of *G. quinquedens* or *G. fenneri* in regard to traps, responses of the spider crab, *Hyas araneus*, and the rock crab, *Cancer irroratus*, to top and side entry traps were reported by Miller (1980). He found success of entry by *C. irroratus* was greater, escapement was reduced, and fewer agonistic encounters occurred in top entry traps. In a complementary study, however, *Cancer productus* had highest

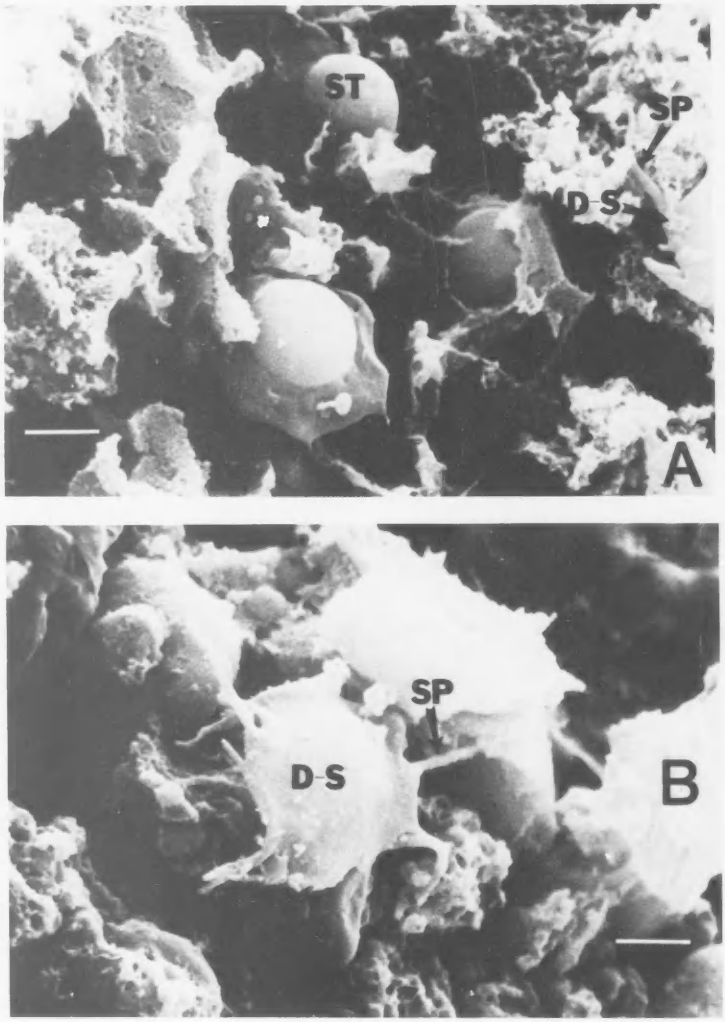

FIGURE 4.—Scanning electron micrograph of testis and vas deferens from male *Geryon fenneri*.
A. Testis: Maturing germ cells (spermatids, ST) surrounded by sustentacular tissue. Developing sperm (D-S), cytoplasmic spike (SP); × 3200. Scale bar 3 μm.
B. Testis: A developing sperm (D-S) possessing partial to fully formed cytoplasmic spikes (SP); × 3200. Scale bar 3 μm.

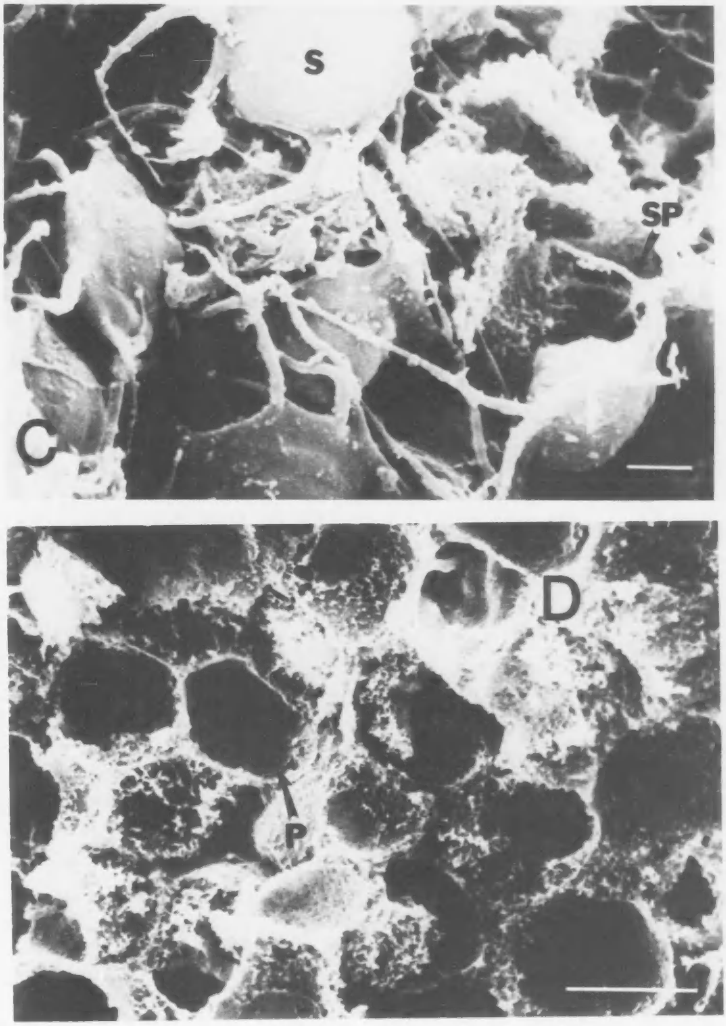

FIGURE 4.—*Continued.*

C. Vas deferens:- Mature multiple stellate sperm (S) showing cytoplasmic spike (SP); × 3840. Scale bar 2 μm.

D. Vas deferens: Pockets (P) within the vas deferens previously occupied by the mature stellate sperm; × 1600. Scale bar 10 μm.

success in entering a side entry trap whose entrances were parallel to the current (Miller 1978). Although our traps were deployed parallel to surface current, their orientation on the bottom relative to bottom current is unknown. We are assuming that golden crabs were successful in locating the entrance and were retained longer in the top entry Florida trap than in the Fathoms Plus trap. It is possible, however, that golden crab were equally or more successful in locating the side entrances of the Fathoms Plus trap but that escapement, especially of smaller golden crab, was higher. This would explain the capture of fewer but larger individuals by the Fathoms Plus trap.

The overwhelming dominance of males in this study contrasts with results reported in other geographic areas for golden crab. Luckhurst (in press) noted that sex ratio in his sample (n = 244) of *G. fenneri* from Bermuda waters was approximately 1:1. Otwell et al. (1984) noted that males tended to be more abundant at greater depths (>540 m) in the Gulf of Mexico; however, they cautioned that trap design may influence the percentage of male crabs caught. Commercial crabbers noted a decline in catch rates and number of male *G. fenneri* with increasing depth on the slope in the eastern Gulf of Mexico (National Marine Fisheries Service fn. 5). We also found increased abundance of females at greater depths, although our results are limited due to the small number of females collected. This is apparently not an artifact of sampling with only the Fathoms Plus trap in the deepest stratum since more females were collected in the Florida trap than with the Fathoms Plus trap when only strata 1-3 were considered. Segregation of the sexes by depth has been observed in several studies of *G. quinquedens*. Wigley et al. (1975) collected more female red crabs than males, but this dominance was limited to intermediate depths (320-503 m). Ganz and Herrmann (1975) similarly noted dominance by male red crab at depths >685 m off Rhode Island. This same pattern was noted for red crab in the vicinity of Norfolk Canyon where females were more abundant than males from depths <600 m (Haefner and Musick 1974; Haefner 1978). In Canadian waters, however, female red crabs were reported by Stone and Bailey (1980) to be considerably less abundant than males. Although they attributed this discrepancy to trap bias, another study in the same general area found females were present but highly contagious in distribution. Whether seasonal migrations related to mating or spawning occur as hypothesized by Wigley et al. (1975) for *G. quinquedens* remains to be substantiated. What is evident from our results is that male *G. fenneri* are dominant in depth strata where catch per unit of effort is highest.

Size-related distribution of *G. fenneri* with depth, similar to that reported for red crab, may occur in the South Atlantic Bight. We found the largest crabs in the shallowest (274-366 m) and deepest (733-823 m) strata. A clear trend of size-related up-slope migration such as Wigley et al. (1975) reported for *G. quinquedens* is not apparent, however, because of trap bias for capture of larger crabs of both sexes. Otwell et al. (1984) also noted no pattern in size of golden crab by depth for either sex. Tagging studies of red crab off southern New England provided no evidence for migration patterns and indicated instead that tagged crabs seldom moved more than 20 km from their site of release (Lux et al. 1982).

The size composition of golden crab from our study showed that crabs become trappable as small as 85 mm CW but that the greatest proportion of trapped individuals is >100 mm CW. Over 90% of all individuals collected exceeded 114 mm CW which is the minimum size of red crab accepted for commercial utilization (Wigley et al. 1975). A much smaller proportion (52%) of golden crab >114 mm was indicated in size-frequency distributions of trap-caught golden crab near Bermuda (Luckhurst in press). Although Otwell et al. (1984) did not present size and weight-frequency data for golden crab in the Gulf of Mexico, they found mean size of male crabs ranged from 155 to 163 mm with mean weight extremes of 1.07-1.15 kg, while females were smaller with mean CW ranging from 119 to 135 mm and mean weight extremes of 0.45-0.50 kg. These data and those from our study suggest that the average size of golden crab from the South Atlantic Bight and Gulf of Mexico is larger than the average size of red crab reported along the eastern United States and Canada. Wigley et al. (1975) reported average width of male *G. quinquedens* was 99 mm with an average weight of 413 g. Average width of all females from their study was 90 mm with a mean weight of 244 g. Comparisons of size composition between the two studies must be qualified, however, by a caveat that differences in sampling methods probably influenced sample statistics. The apparent larger size of golden crab may be better substantiated by maximum width and weight measurements, which for our study were

193 mm and 2,109 g, respectively. These values were markedly larger than those reported for red crab in the vicinity of Norfolk Canyon (Haefner 1978), off northeastern United States (Wigley et al. 1975), or the Scotian Shelf (Stone and Bailey 1980; McElman and Elner 1982).

The small number of females collected during the first year precludes any definitive statements regarding ovarian cycles or spawning patterns. Ovarian developmental stages are similar to those reported by Haefner (1977) for *G. quinquedens*. We also found his use of vulvae condition as an external indicator of copulation to be fairly reliable, but examination of the seminal receptacles for sperm or spermatophores provided the only true indication of mating. Tentative interpretations on ovarian development, vulval condition, and presence of seminal products suggest that females may become sexually mature at 97 mm CW. Haefner (1977) suggested that female *G. quinquedens* become sexually mature within the intermolt size of 80-91 mm CW.

A lack of ovigerous females in our first-year sampling effort could be indicative of a restricted spawning season similar to that reported for red crab (Haefner 1977; Wigley et al. 1975). Absence of ovigerous females from our samples, however, may be related to the small number of female golden crab collected.

Observations on molting and mating of a female (110 mm CW), which had been held in a refrigerated aquarium since February 1986 and had completed ecdysis in late May 1986, confirmed that female golden crab molt just before mating occurs. This behavior, as well as the observed premolt embrace, has been described for *G. longipes* (Mori and Relini 1979), although it has not been reported previously for either *G. quinquedens or G. fenneri*.

Stage of ecdysis is an important factor affecting meat condition and yield in golden crab. Crabs which have recently molted generally have a very poor meat yield and are not marketable[8]. Since most golden crab in the intermolt stage had blackened abraded areas or poecilasmatid barnacles on the exoskeleton, their presence was useful in distinguishing premolt from postmolt crabs which were brighter in color and had few abrasions.

[8]W. Lacy, Seafood Marketing Section, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412, pers. commun. 1985.

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DIFFERENTIATION OF MITOCHONDRIAL DNA IN ATLANTIC HERRING, *CLUPEA HARENGUS*

I. KORNFIELD AND S. M. BOGDANOWICZ[1]

ABSTRACT

To investigate genetic relationships among spawning stocks of Atlantic herring, *Clupea harengus*, in the Gulf of Maine and Gulf of St. Lawrence, mitochondrial DNAs from ripe females at three localities were examined by restriction endonuclease analysis. Using seven variable restriction enzymes, mtDNAs from 69 completely characterized individuals produced 26 composite digestion patterns. The majority of individuals (65%) possessed composites which were common to two or more spawning localities; the other individuals displayed locality specific "unique" composites. Analysis of relationships among these unique composites suggested that some may have been derived from other areas. These results are not consistent with the idea that separate genetic stocks of Atlantic herring exist in the Gulf of Maine.

The relationships among discrete spawning stocks of Atlantic herring, *Clupea harengus*, are problematical. A large number of stocks and stock complexes are recognized throughout the eastern and western North Atlantic; these delineations are based largely on meristic characters, spawning time, and spawning location. Tagging studies in the western North Atlantic have shown extensive migration and mixing of stocks during nonreproductive periods (Creaser et al. 1984). More limited studies of spawning fish have demonstrated that some tagged individuals returned to their spawning locations (Wheeler and Winters 1984). Recent work has advanced the hypothesis that specific environmental attributes essential for growth and survival of larval herring largely determine where Atlantic herring will spawn (Iles and Sinclair 1982). The notion that spawning occurs near areas suitable for larval retention could explain the discontinuous or patchy distribution of spawning areas. Similarly, the occurrence of fall spawning and spring spawning Atlantic herring stocks may be a function of completion of larvae growth and metamorphosis constrained by resources within the larval retention area (Sinclair and Temblay 1984). There is thus a reasonable model to explain the existence of geographically or temporally discrete spawning stocks. However, the genetic structure among these different spawning groups is unresolved.

Implicit in the Atlantic herring stock concept is the idea that individual fish belong to defined groups by virtue of returning to specific spawning sites. If this is the case, there should exist high genetic continuity among individual Atlantic herring within stocks and relatively lower continuity among stocks. That is, genetic differences should be observable among stocks. Unfortunately, meristic characters useful for stock definition are under environmental influence and have a complex genetic basis. Electrophoretic characterization of allozyme variation should potentially permit identification of genetic discontinuities among stocks. However, despite the availability of a large number of polymorphic markers and adequate sample sizes, significant genetic heterogeneity among Atlantic herring stocks has not been demonstrated (Anderson et al. 1981; Kornfield et al. 1982; Grant 1984; Riviere et al. 1985). The inability of allozyme analysis to differentiate among herring stocks could occur for two alternative reasons. Herring stocks could have originated so recently that there has been insufficient time for stock specific allozyme variation to accumulate. Further, natural selection may be acting to homogenize allele frequencies that may characterize stocks. Thus, standard allozyme analyses may not be sufficiently sensitive to detect genetic variation which distinguishes stocks. Alternatively, herring stocks could be largely composed of individuals that do not return to natal spawning sites. Under this explanation, herring stocks would not represent discrete genetic groups but rather random assemblages of spawning individuals. Management of

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exploited herring stocks could differ dramatically depending upon which alternative is correct (MacLean and Evans 1981).

Restriction endonuclease analysis of mitochondrial DNA (mtDNA) has, in recent years, uncovered substantial genetic variation in natural populations (Brown 1983). The technique is potentially much more sensitive than conventional allozyme analysis for characterizing population structure and has been successfully exploited to discriminate groups not detectable with allozymes (e.g., Avise et al. 1986; R. W. Chapman unpubl. data). To further examine genetic relationships among herring stocks, restrictive enzyme digestion patterns of mtDNA were examined in individuals from three spawning localities in the northwestern Atlantic.

MATERIAL AND METHODS

Samples of fall spawning Atlantic herring were obtained from two discrete localities in the Gulf of Maine: Jeffries Ledge, MA (lat. 42°50′N, long. 66°30′W; 9 September 1984) and Trinity Ledge, NB, Canada (lat. 45°20′N, long. 65°30′W, September 1984; 30 August 1985). A sample of spring spawning Atlantic herring was collected from off Pt. Escuminac, Gulf of St. Lawrence, NB (lat. 47°01′N, long. 64°40′W; 12 May 1985) (Fig. 1). All Atlantic herring were collected during peak reproduction. Samples were frozen in the field and stored at −80°C for up to 6 months prior to analysis.

Lansman et al. (1981) provided a useful review of the application of mtDNA to population studies. mtDNA was prepared from egg tissue (11-15 g/female) by the rapid phenol extraction procedure of Chapman and Powers (1984). After the final chloroform extraction, mtDNA in the aqueous phase was precipitated in 95% ethanol in the presence of 3 M sodium acetate, dried under vacuum and dissolved in 10 mM Tris, pH 7.5.

FIGURE 1.—Collection localities for Atlantic herring. (1) Jeffries Ledge, MA; (2) Trinity Ledge, NB; (3) Point Escuminac (St. Lawrence), NB.

Samples were digested with 16 six-base restriction endonucleases (Table 1) under conditions recommended by suppliers (Bethesda Research Labs, New England Biolabs). Just prior to addition of restriction enzymes, samples were incubated with Ribonuclease A (RNase) at 60°C for 5 minutes and allowed to cool to 37°C. Restriction fragments were separated by horizontal electrophoresis in 1% agarose gels. *Hin*dIII digests of lambda DNA were used as molecular weight standards on all gels. Gels were stained for 60 minutes with 0.5 g L^{-1} ethidium bromide and destained for 30 minutes in 5 mM $MgSO_4$ prior to photography. The relative mobilities of mtDNA and lambda fragments were measured from photographs with a stereomicroscope. Molecular weights of restriction fragments were calculated from least squares third order polynomial regressions of log-transformed lambda fragment mobilities.

RESULTS

Restriction digests of mtDNAs prepared by the rapid phenol extraction procedure well resolved, repeatable digestion patterns (Fig. 2). Two enzymes, *Bam*H1 and *Sal*I did not digest the herring mtDNA molecule. Variant digestion patterns were noted for the majority of enzymes examined (Table 1) and were common both within

FIGURE 2.—Ethidium bromide stained agarose gel of mtDNA digestion patterns of Atlantic herring, *Clupea harengus* (lanes 2-8). Samples were digested with *Bst*EII (lanes 2, 3; phenotypes B, C), *Eco*RI (lanes 4, 5; phenotypes A, C), and *Bgl*II (lanes 6, 7; phenotypes A, B). Standard (lanes 1, 8) is a *Hin*dIII digest of lambda DNA.

TABLE 1.—Digestion patterns of Atlantic herring mtDNA produced by six-base restriction endonucleases[1]. Superscripts denote homologous fragments, measured independently.

*Apa*I						*Bst*EII					*Bgl*II			
A	B	C	D	H	I	A	B	C	D	E	A	B	C	D
8,800[a]	8,800[a]	7,200[e]	6,350	8,800[a]	7,350	11,830[d]	10,820[d]	15,160	12,200	11,700[d]	9,940	6,590[d]	14,000	6,600[d]
7,200[e]	6,100[c]	5,300	6,100[c]	7,200[e]	6,100[c]	4,670[a]	4,670[a]	1,150[c]	4,700[a]	3,650	4,130[a]	4,180[a]	1,990[b]	3,900
900[b]	960[d]	3,450	2,450[h]	1,100	2,450[h]	550[b]	1,160[c]	550[b]		1,340	1,990[b]	3,230[e]	1,270[c]	3,250[e]
	900[b]	900[b]	960[d]		900[b]		550[b]			550[b]	1,270[c]	1,960[b]		1,970[b]
			900[b]									1,220[c]		1,220[c]
16,900	16,760	16,850	16,760	17,100	16,800	17,050	17,200	16,860	16,900	17,240	17,330	17,180	17,260	16,940

*Dra*I		*Eco*RI			*Eco*RV				*Hin*dIII	*Kpn*I		*Pst*I
A	B	A	B	C	A	B	C	D	A	A	B	A
7,600	11,370	9,460[a]	14,020	9,400[a]	8,680[a]	8,200	8,600[a]	14,500	13,500	15,200	17,000	10,790
3,700	2,530[a]	4,220	3,130[b]	7,250	6,000	6,490	8,200	2,270[b]	2,820	1,910		5,850
2,570[a]	2,290[b]	3,010[b]			2,230[b]	2,030			1,000			
2,310[b]						1,000						
16,170	16,190	16,690	17,150	16,650	16,910	17,720	16,800	16,770	17,320	17,110	17,000	16,640

*Pvu*II			*Sac*I	*Xba*I	*Xho*I		*Xmn*I
A	B	C	A	A	A	B	A
7,480	12,840	13,600	9,800	5,350	14,000	16,500	7,940
5,590	1,550[a]	1,560[a]	7,300	4,880	2,690		3,780
1,580[a]	1,420[b]	1,400[b]		2,890			2,330
1,420[b]	850[c]			2,060			1,810
900[c]				2,050			1,320
16,970	16,660	16,560	17,100	17,230	16,690	16,500	17,180

[1]Two additional enzymes, *Bam*HI and *Sal*I produced no (or one) cuts.

and among population samples. For polymorphic restriction enzymes, all digestion profiles of variants were consistent with the hypothesis of single nucleotide substitutions. No mtDNA size variants, resulting from additions or deletions of DNA, and recently found in a number of fish groups (Bermingham et al. 1986; R. W. Chapman[2]), were observed.

The mean mtDNA genome size, found by averaging the sums of all digestion patterns (Table 1), was 16,990 bp (base pairs) ± 620 bp (SD). In quantifying molecular size from ethidium bromide stained agarose gels, two constraints must be noted. First, variation associated with measurement of fragment mobilities is inevitable. Because of the nonlinear relationship between fragment mobility and molecular size, slight measurement errors can produce large variations in estimated sizes, particularly for fragments with low mobilities. As a consequence, homologous cleavage fragments (those which consistently exhibit the same mobility on a single agarose gel) may yield different molecular size estimates, e.g., *Apa*I fragment "a", Table 1. Second, mtDNA cleavage fragments less than 500 bp could not be routinely scored on ethidium bromide gels because of their low absolute staining intensities and fluorescent background in this region (Fig. 2). Regardless of the above constraints, individual cleavage fragment phenotypes could be consistently determined.

Seven polymorphic restriction endonucleases (*Apa*I, *Bgl*II, *Bst*EII, *Eco*RI, *Eco*RV, *Pvu*II, and *Xho*I) were used to generate composite digestion patterns for individual Atlantic herring. Twenty-six unique composite digestion patterns were observed in 69 completely characterized individual Atlantic herring. The distribution of these composites with respect to spawning locality is given in Table 2; five common composites (nos. 1-5) were observed to occur at all three spawning localities.

Shared fragment similarity was calculated pairwise for all composites and was used to generate estimates of p, percent sequence divergence (Upholt 1977). Estimated sequence divergence among composites varied considerably, mean = 1.66% +/− 0.91 (SD), range 0.19% − 4.37% (Table 3). Phenetic relationships among composites were examined by UPGMA (Unweighted Pair Group Method of Arithmetic averaging) clustering (Sneath and Sokal 1973) of sequence divergence (Fig. 3). Two major clusters were noted: one involving three composites (5, 17, 26) and the other including all other composites. Composites from both clusters were present in all spawning populations.

A network of relationships among composites was constructed by connecting composites in increments of single site gains or losses to minimize the total number of restriction site changes required (Fig. 4). Sixteen equally parsimonious networks requiring 29 steps were generated. Composite number 1 can be considered central because it is the most common pattern observed and also occurs in the Eastern Atlantic (S. M. Bogdanowicz unpubl. data).

DISCUSSION

Based on the occurrence of geographically disjunct spawning groups and homing of some tagged individuals, it has been tacitly accepted that Atlantic herring stocks are reproductively isolated. The basic analytical premise of this study was that restriction endonuclease analysis

[2]R. W. Chapman, Chesapeake Bay Institute, The Johns Hopkins University, Shandy Side, MD 20764, pers. commun. December 1985.

TABLE 2.—Distribution of mtDNA composite digestion patterns in samples of Atlantic herring.

Composite designation	Composite mtDNA digestion pattern[1]	Jeffries Ledge	Trinity Ledge		St. Lawrence
			1984	1985	
1	AAAAAAA	5		2	5
2	AABAAAA	2	2	2	6
3	BAAAAAA	2		3	6
4	AABAAAB	1	1	3	1
5	ABAABAA	1	1	2	1
6	BABAAAA	1			
7	AABACAA			1	1
8	AAAADAB	1			
9	IAAAAAA				2
10	DAAAAAA				1
11	CAAAABA				1
12	BAEAAAA				1
13	HABAAAA				1
14	AAAAABB		1		
15	CAAAAAA		1		
16	BABAAAB		1		
17	ABABBAA		1		
18	ABBACAA			1	
19	AAACCAA			1	
20	IABAAAA			1	
21	AACAAAA			1	
22	BADAAAA			1	
23	CABAAAA			1	
24	AADAAAA			1	
25	ACDAAAA			1	
26	ADDABAA			1	
		13	8	22	26

[1]Letters (from left to right) are digestion patterns for *Apa*I, *Bgl*II, *Bst*EII, *Eco*RI, *Eco*RV, *Kpn*I, and *Xho*I (Table 1).

TABLE 3.—Estimated percent sequence diverg

	1	2	3	4	5	6	7	8	9	10	11	12	1
1	—	0.42	0.42	0.91	1.40	0.86	0.91	0.97	0.73	0.87	0.91	0.87	0.
2		—	0.87	0.42	1.54	0.69	0.42	1.49	0.87	1.33	1.40	1.68	0.
3			—	1.40	1.92	0.40	1.40	1.49	0.56	0.40	1.40	0.40	0.
4				—	2.62	0.87	0.91	0.97	1.40	1.92	2.47	1.92	0.
5					—	2.90	2.62	1.49	2.32	2.90	3.09	2.90	1.
6						—	0.56	2.04	0.69	0.82	1.92	1.13	1.
7							—	1.74	1.40	1.92	2.04	1.92	0.
8								—	1.89	2.04	2.64	2.04	1.
9									—	0.40	1.06	1.00	1.
10										—	1.19	1.13	1.
11											—	2.32	1.
12												—	1.
13													
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divergence among mtDNA composites in Atlantic herring.

12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
0.87	0.14	0.97	0.73	1.40	2.04	1.40	0.97	1.19	0.59	0.91	1.19	0.45	0.97	2.47
1.68	0.27	1.49	0.87	1.19	1.78	0.87	1.49	0.69	0.42	0.73	0.40	0.29	0.77	2.62
0.40	0.56	1.49	0.87	0.87	2.62	1.92	1.49	1.00	1.06	0.42	1.32	0.91	1.49	3.09
1.92	0.73	0.97	1.78	0.42	3.47	1.40	1.74	1.19	0.91	1.63	0.87	1.12	1.74	3.46
2.90	1.92	3.31	2.32	3.76	0.42	1.54	1.89	3.38	2.62	3.61	2.90	2.47	2.80	0.73
1.13	1.00	2.04	1.32	0.40	3.24	1.33	2.04	0.53	0.87	0.56	0.82	1.06	1.63	3.76
1.92	0.73	2.17	1.40	1.40	2.47	0.42	0.97	1.19	0.91	1.63	0.87	1.12	1.74	3.47
2.04	1.49	0.32	1.49	1.49	2.64	2.32	1.42	2.47	1.74	2.17	2.04	1.58	2.32	3.16
1.00	1.19	1.89	0.87	1.19	3.09	1.92	1.89	0.13	1.40	1.06	1.00	1.26	1.89	3.61
1.13	1.33	2.04	1.00	1.33	3.24	2.46	1.63	0.53	1.19	0.56	1.13	1.06	1.63	3.24
2.32	1.78	1.34	0.42	3.09	3.47	2.62	2.17	1.92	1.63	2.04	0.87	1.49	2.17	4.04
—	1.33	2.47	1.33	1.33	3.24	2.46	2.04	1.46	1.19	0.87	1.81	1.40	2.04	3.76
	—	1.49	0.87	1.19	3.09	1.19	1.49	1.00	0.73	1.40	0.69	0.91	1.49	3.09
		—	1.49	1.12	3.73	1.89	2.32	2.47	1.74	2.17	2.04	1.58	2.32	4.37
			—	1.54	2.18	1.92	1.49	1.33	1.06	1.40	0.40	0.91	1.49	3.09
				—	3.09	1.92	2.80	1.00	1.40	1.06	1.33	1.63	2.32	4.19
					—	2.18	2.64	4.33	3.47	4.04	3.76	3.89	3.73	1.26
						—	1.49	1.68	1.40	2.18	1.33	1.63	1.89	1.78
							—	2.47	1.74	2.17	2.04	1.58	2.32	3.16
								—	1.54	1.19	0.82	1.40	2.04	3.76
									—	1.26	0.87	0.77	1.34	2.95
										—	1.54	0.45	0.97	2.47
											—	1.06	1.63	3.24
												—	0.47	1.89
													—	1.73
														—

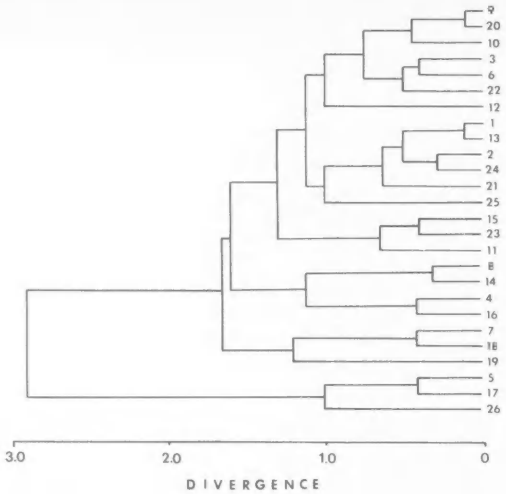

FIGURE 3.—Phenetic relationships among mtDNA composite cleavage patterns of Atlantic herring. Estimates of sequence divergence were clustered by UPGMA.

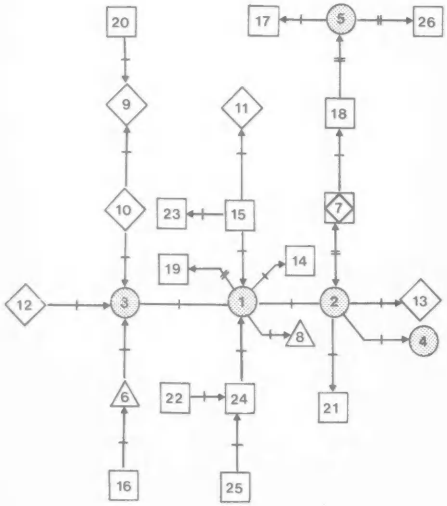

FIGURE 4.—Cladistic relationships of 26 composite cleavage patterns of Atlantic herring mtDNA. Composites are connected parsimoniously to minimize the number of restriction site changes required. Shaded numbers refer to composites observed at all three spawning locations. Crossbars on connecting lines indicate minimum number of site changes required to connect adjacent composites; arrows indicate direction of site losses. Locality symbols: square - Trinity Ledge; triangle - Jeffries Ledge; diamond - St. Lawrence.

of mtDNA should have been able to differentiate among such reproductively isolated populations. However, the spawning groups studied were not fully distinguishable by composite mtDNA digestion patterns generated by six-base restriction endonucleases; no absolute stock markers were present. Six of the twenty-six composite designations, representing more than 65% of all individuals, were shared by at least two geographically distinct spawing groups.

The occurrence of common composites in all spawning populations could occur for at least two reasons: First, commonality could reflect recent and/or ongoing gene exchange among populations. Consistent with this idea, there is no association between frequencies of common composites (nos. 1-5) and spawning locality ($G = 6.29$, p 0.5, Sokal and Rohlf 1981). As is generally acknowledged, small numbers of individuals migrating among populations are sufficient to homogenize different groups (Allendorf 1983). The absence of two common composites (1 and 3) in the 1984 Trinity Ledge sample might be due to the stochastic effect of small sample size, though this observation could also imply some element of temporal instability in composition. Second, and alternatively, these common composites could represent ancestral mtDNAs which were widespread prior to any genetic isolation of populations. That is,

the occurrence of common composites need not imply current gene exchange (Avise et al. 1984; Neigel and Avise 1986); population sizes are sufficiently large to support the co-occurrence of common ancestral composites and their derivatives.

The presence of 20 composites which were specific to spawning groups suggests that there may be some degree of genetic isolation among stocks. Given the limited number of individuals sampled, it is difficult to know whether "unique" composites are actually restricted to specific stocks. For example, rather than increasing the abundance of previously observed unique composites, the second sample from Trinity Ledge generated additional composites. There is thus little indication that "unique" composites may be useful in defining stocks. The great composite diversity displayed in the samples of Atlantic herring most probably reflects the very large population sizes involved.

In the absence of gene flow among spawning populations, we would expect a unique composite to be found in the same population as its most probable precursor. In three out of seven instances, precursors of unique composites occurred in different spawning populations (this result holds for all other equally parsimonious networks). For example, composite 9, which only occurs in the St. Lawrence sample, is the immediate ancestor of composite 20 from Trinity Ledge. In addition, the two unique composites which were maximally divergent (12 steps) occurred in the same population (Trinity Ledge 1985). These considerations, as well as the absence of any consistent geographic pattern of unique composites are consistent with the idea of gene flow.

Evidence for the ability of mtDNA analysis to detect subtle population differentiation is compelling (Avise et al. 1979; Lansman et al. 1981; Wilson et al. 1985; Bermingham and Avise 1986). However, since differentiation of mtDNA restriction patterns is a time dependent process (Kessler and Avise 1985), it is possible that there has been insufficient time to accumulate population specific differences in Atlantic herring (Grant 1984, 1985). Atlantic herring stocks, as they currently exist, can not predate the origin of the Gulf of Maine following glacial withdrawal 18,000 years ago (Kellogg 1980). In addition, since the effective population sizes of Atlantic herring stocks are very large, they would be expected to diverge only very slowly by lineage sorting (Neigel and Avise 1986).

Consistent, significant genetic differences among spawning groups of Atlantic herring is a sufficient, but not a necessary, condition to regard populations as discrete stocks. Our results do not support the hypothesis that discrete Atlantic herring stocks exist throughout the Gulf of Maine; however, the absence of such differences does not allow us to rigorously conclude that there is gene flow among the populations in question. More comprehensive sampling of mtDNA composites within and among populations in the western North Atlantic may better allow resolution of this problem. Regardless, for the sake of preserving variability, resources like the Atlantic herring should be managed under the assumption that every spawning group is a semi-discrete genetic entity.

ACKNOWLEDGMENTS

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POPULATION AND FISHERY CHARACTERISTICS OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*

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ABSTRACT

A stock assessment analysis of the Atlantic menhaden, *Brevoortia tyrannus*, fishery was conducted with purse seine landings data from 1940 to 1981 and port sampling data from 1955 to 1981. Virtual population (cohort) analysis was used to estimate historical stock sizes, rates of fishing, and numbers of recruits. The population exploitation rate (age 1 and older) ranged from 0.29 to 0.51 and averaged about 0.38 for the 1955-79 period. Recruitment at age 0.5 during the 1955-79 period ranged from 1.5 to 18.6 billion fish, with a mean of 5.1 billion. Classical spawner-recruitment relationships describe the data poorly. Growth and mortality data were used to examine yield per recruit for temporal and geographic fishing areas and for the entire fishery. Size at age data, while supporting an earlier hypothesis of density-dependent growth, show a trend toward slower apparent growth in the 1970's than is explained by this hypothesis alone. Yield per recruit of Atlantic menhaden dropped from 107 g for the 1970-72 period to 57 g for the 1976-78 period. A Graham-Schaefer production model estimate of maximum sustainable yield (MSY) for the 1955-79 period was 414,000 metric tons. A modified Pella-Tomlinson production model provided a MSY estimate of 557,000 metric tons. The latter estimate is probably unattainable given current temporal and geographic fishing patterns. Results of these analyses indicate that the Atlantic menhaden fishery suffers from growth overfishing.

Some fishing activity has been conducted on Atlantic menhaden, *Brevoortia tyrannus*, since colonial times, but the purse seine fishery and factory reduction activities began in New England about 1850 (Reintjes 1969). The geographic range of the modern reduction fishery was established by the 1930's (Nicholson 1971a) and the fishery underwent substantial expansion following World War II. Good discussions of the actual fishing operations and types of gear involved are contained in Reintjes (1969) and Nicholson (1971a).

With the exception of the 1950 fishing season, the Atlantic menhaden fishery has dominated total U.S. fishery landings in volume since 1946, when the Pacific sardine, *Sardinops sagax*, fishery was declining. This dominance continued until 1963, when, during its own decline, Atlantic menhaden landings were surpassed by the gulf menhaden, *Brevoortia patronus*, purse seine fishery. Gulf menhaden landings have dominated U.S. fishery landings since, and Atlantic menhaden currently account for about one-third of the total menhaden landings.

The U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries[3] began biological investigations on Atlantic menhaden in 1952. Studies were initiated during what were, in retrospect, peak landing years with the goal to determine the nature of population fluctuations and variability in geographic abundance (June and Reintjes 1959). Following the marked reduction in stock abundance that occurred in the late 1960's, studies were initiated to determine probable causes for the decline and to develop management options to avert a second decline.

The fishery for this migratory clupeid takes place primarily within states' jurisdictional waters (<3 miles from shore), and managerial authority rests with the individual states. Coastwide management plans are cooperatively formulated under the auspices of the Atlantic States Marine Fisheries Commission (ASMFC), but the implementation requires separate legislative or regulatory action by each member state. Individual states are not obligated to act upon cooperatively derived plans or management actions from the ASMFC.

Stock assessment studies provide fundamental scientific information required to formulate coastwide management actions. An early evaluation of the stock status of Atlantic menhaden,

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covering the 1955-68 fishing seasons, was prepared by Henry (1971). Applying virtual population methods (number of fish alive that will be caught in the future (Ricker 1958)) to landings from 1955 to 1969, Schaaf and Huntsman (1972) conducted additional analyses of the population dynamics of this resource. Stock status was again examined with production models using adjusted effort and landings through 1973 (Schaaf 1975a). Population dynamics and potential yield of Atlantic menhaden were further examined by Schaaf (1979), using estimates of numbers landed through the 1976 season; he also employed cohort analysis with Pope's (1972) approximation and the Leslie matrix (after Leslie 1945). In response to a request from the State/Federal Fishery Management Program, Atlantic Menhaden Scientific and Statistical committee, a population dynamics subcommittee was formed (Federal, state, and industry membership). Their report (ASMFC[4]) contained an indepth stock assessment (conducted by the Southeast Fisheries Center (SEFC) Beaufort Laboratory, NMFS) based on landings data through the 1977 season, and was the basis for the Atlantic menhaden management plan adopted by the ASMFC (ASMFC 1981). A computer simulation model of the fishery was developed in an independent analysis and was based on the 1965 through 1978 seasons (Reish et al. 1985; Ruppert et al. 1985). The general concensus of the earlier studies (Henry 1971; Schaaf and Huntsman 1972; Schaaf 1979; ASMFC fn. 4) was that the Atlantic menhaden stock was being overexploited and concern was expressed regarding the reduced spawning stock and/or the high rate of harvest of immature fish.

The primary objective of this report is to evaluate the stock status of Atlantic menhaden through the 1981 season. The more recent 1970-78 fishing seasons are emphasized, notably in presentations of yield per recruit. Effort, landings, and biological sampling data from 1955 through 1981 are used to estimate historic population sizes, age-specific rates of fishing mortality, actual and potential fishery yield, and to examine the spawner-recruitment relationship.

The secondary objective is to determine what historical series of events led to recent conditions in the fishery. This objective can be reasonably met by examining the geographic patterns of harvesting rates and the relative amount of effort expended in each geographic area.

The final objective is to generate some information on the relative abundance and age structure of the menhaden stock during the earlier, presampling period of 1940-54. This is accomplished by comparing, with inferences, the geographic patterns of harvest and effort distribution from the time period with port sampling data (and thus estimates of age-specific exploitation rates) to the patterns of an earlier period when only landings and effort data are available.

OVERVIEW OF LIFE HISTORY AND STOCK STRUCTURE

Hypotheses of the seasonal distribution and migration patterns of adult menhaden were formulated from observations of fish schools (June and Reintjes 1959; Roithmayr 1963) and analysis of age-length distributions (Nicholson 1971b). These hypotheses were later supported by results of tagging studies (Dryfoos et al. 1973; Nicholson 1978). Much of the population is believed to overwinter south of Cape Hatteras to northern Florida, and in late winter begins moving north. By summer, adult menhaden are normally found in dense schools in open coastal waters, bays, and sounds from northern Florida to Maine. These fish schools are stratified by age and size, with the average length and weight increasing with increasing latitude. In September, the most northerly portion of the population begins a southerly movement. During November, most of the adult population that summered in waters north of Chesapeake Bay move south around Cape Hatteras. These larger fish are followed in early December by a southward migration of young of the year that have emigrated from estuarine systems north of Cape Hatteras.

Atlantic menhaden spawning occurs to some degree during virtually the entire year, but not over the entire range at any given time. Evidence for this comes from an ovarian maturation study (Higham and Nicholson 1964) and observed distributions of menhaden eggs and larvae on the continental shelf (Reintjes 1969; Chapoton[5]; Kendall and Reintjes 1975; Judy and Lewis

[4]ASMFC (1980). Report of the Atlantic Menhaden Population Dynamics Subcommittee to the Atlantic Menhaden Scientific and Statistical Committee on the status of the Atlantic menhaden stock and fishery. Unpubl. Rep., 68 p. Atlantic States Marine Fisheries Commission, 1717 Massachusetts Ave., N.W., Washington, D.C. 20036.

[5]Chapoton, R. B. 1972. On the distribution of Atlantic menhaden eggs, larvae, and adults. Unpubl. manuscr., 76 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

1983). These authors inferred that menhaden spawn in waters north of Long Island from May to September, in the Middle Atlantic Bight south of Long Island from March through May and again in September and October, but primarily spawn in the South Atlantic Bight from October through March.

Menhaden are believed to spawn in neritic waters over most of the continental shelf, as well as in bays and sounds in the Long Island waters and northward (Reintjes and Pacheco 1966; Nelson et al. 1977; Ferraro 1980). Higham and Nicholson (1964) concluded that menhaden do not spawn inside Chesapeake Bay. The buoyant eggs normally hatch in about 2 days, and the larvae have absorbed their yolk sac in about 4 days at a length of about 5 mm (Kuntz and Radcliffe 1917). The larvae subsequently enter estuarine systems when they are 10-34 mm long (June and Chamberlin 1959; Reintjes and Pacheco 1966; Lewis and Mann 1971). The seasonality of larval immigration varies among geographical sites within years and also among years at the same site, owing at least, in part to environmental conditions. Immigration of larvae has been observed from November through April in the South Atlantic Bight, October to June in the Middle Atlantic and Chesapeake Bay areas, and May to October in waters of Long Island and northward (see Reintjes and Pacheco 1966 for literature summary; Lewis and Mann 1971).

Following entry into estuarine waters, larvae progress to lower salinity waters and are frequently found in high abundance in smaller tributary estuaries, where they metamorphose into juveniles at a length of about 34 mm (June and Chamberlin 1959; Wilkens and Lewis 1971; Lewis et al. 1972). Young of the year generally remain in estuaries until the fall when most migrate downstream to larger rivers, bays, sounds, and into the ocean. The range in length of juveniles in the fall has been observed from 40 to 185 mm (Kroger et al. 1974). After their estuarine emigration in the late fall and early winter, juvenile menhaden from New England to the northern portion of the South Atlantic Bight migrate southward in dense schools often very close to shore (surf zone) (Kroger et al. 1971; Kroger and Guthrie 1973).

There are debates whether the Atlantic menhaden population is composed of more than one stock (June 1958, 1965; Sutherland 1963; June and Nicholson 1964; Nicholson 1972, 1978; Epperly 1981). However, the apparently similar movement patterns make what potentially may be genetically different spawning groups inseparable in the fishery. Hence, the menhaden population is currently treated as one exploited and managerial stock.

FISHERY DATA BASE

Records of landings of Atlantic menhaden taken by purse seine and the level of effort expended (vessel weeks) have been collected and maintained back to 1940. Early summaries (through 1971) are available from Nicholson (1971a, 1975) and more recently (through 1984) from Smith et al. (in press) (Fig. 1).

Fishery landings have been sampled and numbers at age landed estimated since 1955. The basic sampling methodology used was described by June and Reintjes (1959), with some recent modifications of sample size (Chester 1984). The efficacy and statistical design of the sampling methods are treated in detail by Chester (1984). The aging technique is described by June and Roithmayr (1960). Estimates of numbers at age landed for the 1955-64 seasons are available by fishing area on an annual basis only and are summarized by Nicholson (1975). Estimates of numbers at age landed used in this report for the 1965-81 seasons were available on a subseasonal basis (weekly) but varied slightly from some published annual summaries (Nicholson 1975 [through 1971]; Schaaf 1979 [through 1976]; and ASMFC 1981 [through 1980]) because of rounding differences, biostatistical error corrections, and use of a different estimation methodology[6]. Smith et al. (in press) gave landings at age values for 1965-84. Values we used were similar except that the 1970-81 values given in Smith et al. (in press) reflect minor corrections to the data file which were made subsequent to these analyses.

Size at age data were available from the port sampling data. Summaries of length and weight by age and geographic area are in Nicholson (1975) and more recently, Smith et al. (in press). Detailed treatment of seasonal length and age distributions by geographic area are contained in Nicholson (1971b, 1972).

[6]Some of the landing estimates (1965-1976) used in the development of ASMFC 1981 were obtained from an estimation procedure which used standardized, noncalendar weeks. While this procedure had some advantages relative to accuracy, it was not fully adaptable to the NMFS port sampling design. It was deemed more desirable to maintain a continuous set relative to estimation procedure. The differences are not large enough to alter analytical conclusions.

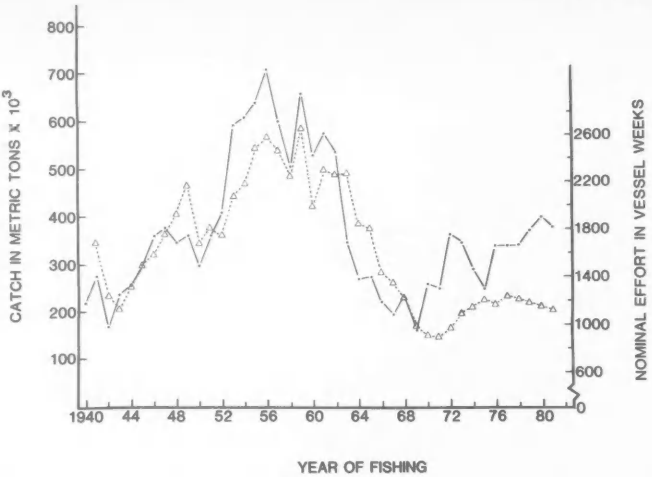

FIGURE 1.—Catch of Atlantic menhaden in thousands of metric tons from 1940 to 1981 (solid line) and fishing effort in vessel weeks from 1941 to 1981 (dashed line). Effort data from 1941 to 1968 are from Nicholson (1971a), catch and effort data from 1968 to 1981 are from Smith et al. (in press).

DESCRIPTION OF THE FISHERY

Geographic Fishing Areas

For purposes of summarization and analysis, June and Reintjes (1959) divided the U.S. Atlantic coast into four geographic fishing areas and one temporal fishing area (Fig. 2). With only a change in the boundary line between the south Atlantic and Chesapeake Bay areas (Nicholson 1975), these divisions have continued to be useful to date.

North Atlantic Area: Waters along the southern coast of Long Island, east of a line due south of Moriches Inlet, and waters northward.

Middle Atlantic Area: Waters west of a line running due south of Moriches Inlet (lat. 40°46′N, long. 72°44′W) on the southern coast of Long Island, southward to Great Machipongo Inlet, VA.

Chesapeake Bay Area: Chesapeake Bay proper and coastal waters south of Great Machipongo Inlet, VA (lat. 37°22′N, long. 75°43′W) to 36°20′N on the North Carolina coast.

South Atlantic Area: Coastal waters of North Carolina south of lat. 36°20′N to Cape Canaveral, FL.

North Carolina Fall Fishery: A temporal fishing area consisting of waters from Cape Hatteras south to the southern border of North Carolina, beginning some time between the last week of October and the second week of November, depending on the arrival of migratory menhaden from more northerly waters, to the end of February of the next calendar year (fishing usually stops by mid-January). For standardized data summary, the week of each season that ends between 8 and 14 November is taken to be the first week of the fall fishery.

Geographic Fishing Seasons

With the exception of state jurisdictional waters in the Chesapeake Bay area, the beginning and ending of seasonal fishing activities were determined by weather and the abundance of fish. Hence, the seasons were somewhat variable. Fishing normally began earlier and ended later in the year in the south Atlantic area, with progressively later beginnings and earlier endings proceeding northward. The south Atlantic (summer) fishery usually began in late March or April and normally ceased in late October or early November. Fishing in waters adjacent to Chesapeake Bay usually began about mid-May and ceased in November, but it occasionally persisted to early December. In the middle Atlantic

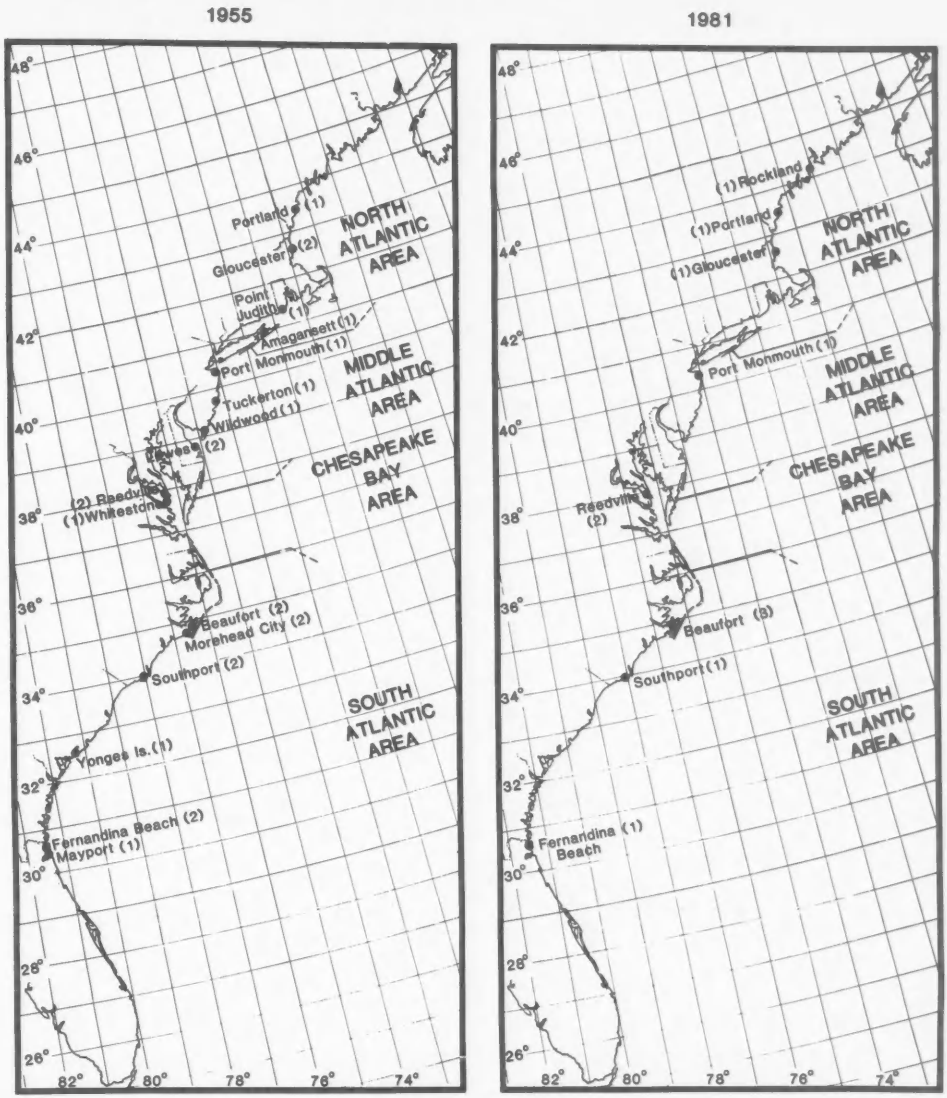

FIGURE 2.—Geographic fishing areas for the Atlantic menhaden purse seine fishery, and landing ports for 1955 and 1981 seasons. The number of plants operating at each port is given in parentheses.

area, fishing usually began about middle to late May and continued into late October. Fishing in the north Atlantic area usually commenced in late May to mid June and continued until mid-September or early October. Current state regulation opens the fishing season in Virginia waters of Chesapeake Bay on the third Monday in May and closes the season on the third Friday in November. All territorial waters of Maryland are closed to purse seine fishing the entire year.

Location and Number of Reduction Plants and Number of Vessels in Purse Seine Fishery

During 1955, 23 plants operated at 16 ports along the U.S. Atlantic coast from Maine to Florida. By 1981 this number had been reduced to 11 plants operating from 8 ports (Fig. 2). The number of vessels landing fish declined from 150 during the 1955 season to 64 by 1967 (Table 1). During 1981, 57 purse seine vessels landed menhaden.

TABLE 1.—Number of purse seine vessels that landed Atlantic menhaden during the fishing year by area, 1955-81 (from ASMFC 1981).

Year	North Atlantic[1]	Middle Atlantic	Chesapeake Bay[2]	South Atlantic[3]	Total[4]	Fall fishery
1955	39	48	20	34	150	51
1956	40	47	24	30	149	63
1957	33	46	25	31	144	64
1958	23	44	28	26	130	63
1959	34	45	31	25	144	59
1960	19	47	22	20	115	37
1961	21	47	23	20	117	44
1962	20	47	29	15	112	49
1963	10	46	36	16	112	46
1964	9	37	38	16	111	51
1965	6	13	38	19	84	46
1966	5	10	36	16	76	43
1967	0	4	32	16	64	46
1968	2	4	25	16	59	45
1969	3	4	22	16	51	36
1970	4	1	18	11	54	37
1971	5	2	20	11	51	32
1972	9	4	19	11	51	5
1973	10	6	23	11	58	4
1974	12	6	22	12	63	12
1975	9	5	22	14	61	17
1976	12	4	21	12	62	13
1977	12	5	24	10	64	16
1978	13	5	22	11	53	18
1979	11	4	22	13	54	18
1980	5	6	24	12	51	19
1981	8	7	23	13	57	19

[1]Vessels fishing from New England ports in recent years are all trawlers that convert to purse seine in summer. Some fish regularly and others sporadically.
[2]Vessels that fished only in regular season. Does not include vessels added in October and November.
[3]Includes only vessels that landed regularly in the summer fishery.
[4]Includes all vessels that landed fish during the year.

Trends in Nominal Effort, Landings, and Age Composition

Since the early 1940's, the Atlantic menhaden fishery has displayed a somewhat classical harvest pattern with an historic increase to a record high, fluctuations, decline, and a secondary slower regrowth (Fig. 1). After an initial slight decline, landings of Atlantic menhaden steadily increased from 167,200 t in 1942 through 1947. Nominal effort generally paralleled landings, but slightly lagged, from a low in 1943 to a minor peak in 1951 and rose to the record high of 712,100 t in 1956. Effort levels increased again in 1953 and reached a secondary peak in 1956 as well. Effort reached its highest level in 1959 with landings at their second highest level of 659,100 t. Landings dropped precipitously from 1962 to a record low 161,600 t in 1969, while effort dropped from 1964 and bottomed in 1971. Although fluctuating, landings showed a net increase from 1970 through 1981. Effort slowly increased up to 1977 and then began a declining trend.

All of the five fishing areas showed a net increase in catches from the 1940's to the peak year in 1956 (Fig. 3). But, the increase was disproportionately distributed between fishing areas. The middle Atlantic area showed the greatest relative increase, followed by the north Atlantic and Chesapeake Bay areas, with the south Atlantic and North Carolina fall fishery only showing slight increases (Fig. 4). While 1956 represented the year of peak landings for the fishery, only the middle Atlantic catches peaked during this year.

The increase in fishing effort expended during the 1940's to the mid-1950's was also disproportionately distributed between fishing areas, with the middle Atlantic showing the greatest increase, followed by the north Atlantic (Fig. 5). The Chesapeake Bay area showed a slight increase, while the south Atlantic and North Carolina fall fishery areas showed little, if any, actual increase in nominal effort.

Following 1956, the proportion of the catch taken in the middle Atlantic area decreased relative to the proportion of effort expended in that area. After 1962, effort (and catches) rapidly decreased in the middle Atlantic area, with both the effort and catches seemingly shifted to the Chesapeake Bay area (Figs. 4, 5). This was a relatively dramatic shift, considering that the middle Atlantic catch was generally dominated by age-2 and -3 fish while Chesapeake Bay catches were dominated by ages 1 and 2. Additionally, middle Atlantic fish were generally larger for any given age than those from Chesapeake Bay. Catches and effort also decreased in the north Atlantic area during the same time frame.

The Atlantic menhaden stock probably had its strongest and broadest age structure in 1955 and 1956, which also represent the first years when port sampling covered the full geographic range

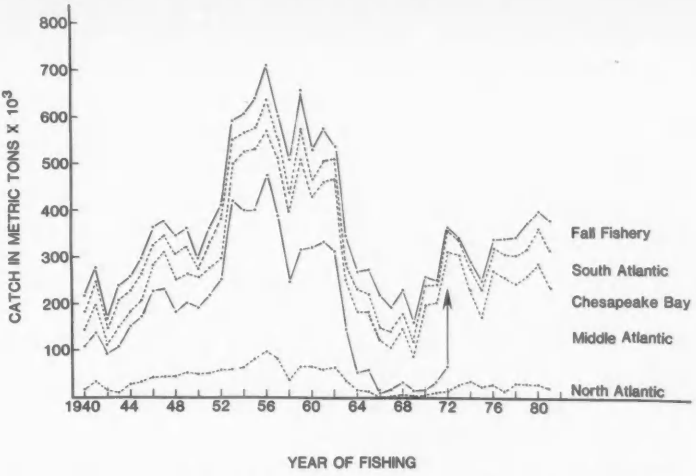

FIGURE 3.—Contribution to landings of Atlantic menhaden by fishing area and season in thousands of metric tons for years 1940-81. The middle Atlantic and Chesapeake Bay area landings are combined after 1972 due to confidentiality restrictions.

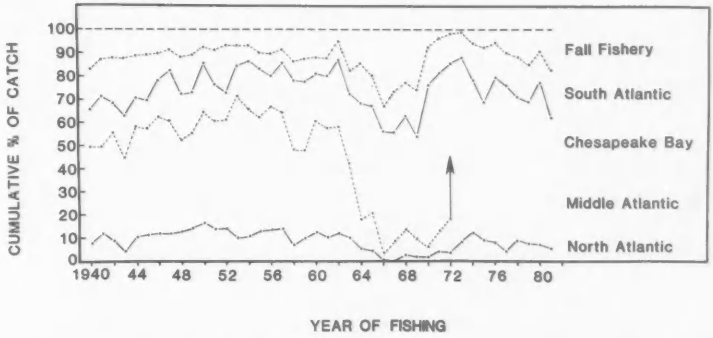

FIGURE 4.—Cumulative contribution by percent total landings of Atlantic menhaden by fishing area for years 1940-81. The middle Atlantic and Chesapeake Bay area values are combined after 1972 due to confidentiality restrictions.

of the fishery (Fig. 6). The number of older fish in the population was somewhat reduced by 1959, but showed a slight recovery in 1960. The age structure became markedly constricted by 1965, and drastically truncated by 1967. The age structure appeared to begin broadening slowly about 1972, and appears to be continuing this trend through 1981.

Although a few individuals aged 9 and 10 years were taken by the fishery during the late 1950's, the maximum age class with adequate representation for computational purposes is age 8. (Hence, the age category of 8+ is taken in this report to be age 8, which for most years contained only age-8 fish.) Individuals age 8+ were represented in landings from 1955 through 1966 fishing seasons. From 1967 through 1969 the oldest fish were age 6, and likewise; 1970 through 1974, 1976, and 1978, age 5; and again, 1975 and 1977, and 1978 through 1981, age 6.

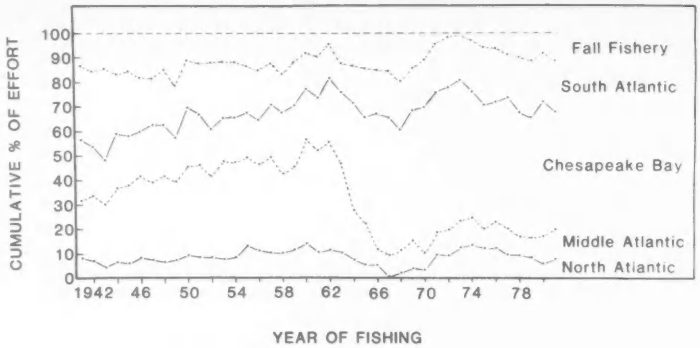

FIGURE 5.—Cumulative fishing effort on Atlantic menhaden as a percent of total, by fishing area for years 1941-81. (Data for 1941 through 1968 were adjusted (reduced) by Nicholson (1971a) to compensate for the small size of vessels that frequently fished in that area. The data for the middle Atlantic area were also adjusted, but to a lesser degree. Data from 1969 to 1981 are unadjusted. North Atlantic area data, adjusted by the Nicholson (1971a) criteria, would probably be less than half the amount shown, while the middle Atlantic area values may only be slightly reduced.)

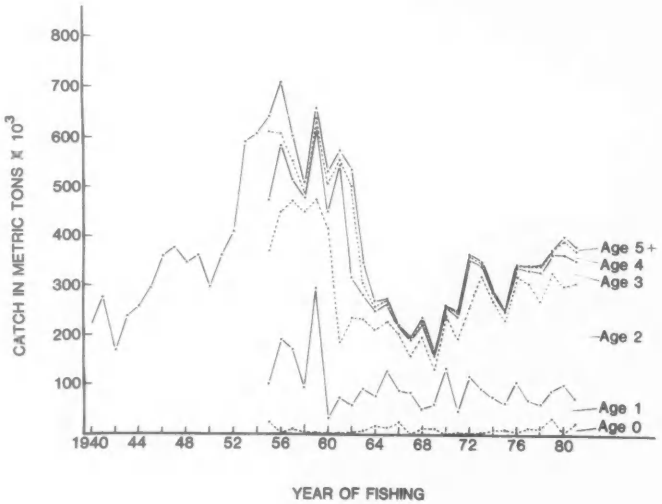

FIGURE 6.—Catch of Atlantic menhaden in thousands of metric tons by age group for 1955 to 1981.

SIZE AT AGE AND GROWTH ANALYSIS

It is necessary to derive two types of size at age and growth estimates because of the seasonal differential distribution of Atlantic menhaden by age and size (Nicholson 1972, 1978). Parameters are estimated by area to characterize the segments of the population normally harvested within that area and are estimated for the entire fishery to characterize the harvested population. Because relative harvest rates may vary among areas between seasons, apparent area-specific growth parameters are estimated for yield-per-

recruit analyses. On the other hand, parameters generated in each area are inappropriate (biased) for describing the entire population (or fishery). For example, growth rates and average size at age values for the north Atlantic area will be greater than those for the population, and similarly values estimated for the south Atlantic will be less than true population values. (The only exception is the North Carolina fall fishery, which apparently harvests a reasonably well-mixed migratory population.)

Size at age and growth estimates for the entire stock are needed for yield-per-recruit analysis for the entire fishery and to ascribe an average size at age for the spawning stock for each year. These estimates are obtained by appropriately weighting the sampling results from each fishing area, as will be shown.

Additionally, since growth of Atlantic menhaden has been shown to be inversely related to year class size (density-dependent) (ASMFC fn. 4), a condition predicated during the estuarine portion of the life cycle (Reish et al. 1985), growth equations must be computed for each year class. The fishing season is divided into quarterly increments for these analyses (Table 2). The analytical steps taken to obtain these size estimates and how they are used follows.

TABLE 2.—Quarterly time increments used in stock assessment analysis of Atlantic menhaden.

Quarter	Beginning week ending date	Ending week ending date
1	≥ 3/01	≤ 5/30
2	≥ 5/31	≤ 8/29
3	≥ 8/30	≤ 11/28
4	≥11/29	≤[1]14/29

[1]February of next calendar year, but same season.

Area-Specific Mean Size at Age and Growth Rates

Mean lengths at age by area by quarter for each of the 1965-81 seasons were estimated directly from the port sampling data as unweighted arithmetic means. These results were in turn arranged by specific year class and fitted to the von Bertalanffy growth equation using the computer package BGC3 (Abramson 1971). It was assumed that each mean length estimate was representative of the middle of the quarterly interval, i.e., for the first quarter (age X.0-X.25) the mean value is assigned to age X.125, etc. These fitted area-specific von Bertalanffy parameters were used to derive estimates of length at age for the beginning of each time interval. These estimates were in turn converted to estimates of weight at age for the area-specific yield-per-recruit analysis.

Mean Size at Age and Growth for the Entire Fishery

Predictive equations for growth which are representative of the population as a whole (entire fishery) are needed to estimate size at age for the spawning stock and for yield-per-recruit analysis of the entire fishery. For years 1965 to 1981, mean lengths at age by quarter for the entire fishery were obtained by weighting each area's estimate of mean length by its corresponding catch in numbers at age by quarter. Age 0.875 (fourth quarter age 0) was the youngest age for which mean length was calculated. These values were arranged by year class and were fitted to the von Bertalanffy growth equation.

Estimates of weighted mean length by quarter could not be calculated for the fish caught before 1965 because estimates of numbers at age landed by quarter by area were not available even though size at age is available weekly. Since much of the fourth quarter catch of the North Carolina fall fishery is composed of migratory stocks, it was presumed that a representative estimate of length at age for the entire population might be obtained from the fourth quarter values from this area alone. To test this hypothesis, mean lengths for the 1965 to 1978 year classes from the fourth quarter in the North Carolina fall fishery were fitted to the von Bertalanffy growth equation. The resultant curves were compared visually with results when all weighted mean length values were used. The results were quite similar when five or more data points were available and dissimilar to relative degrees when <5 data points were available. Because all year classes from 1955 to 1964 had at least 5 data points which met the above criteria, von Bertalanffy curves were fitted to these values (Table 3).

Weight-Length Relationship

The predictive growth equation used in this report uses length at age. Weight-length relationships were derived to estimate weight at age values. The greatest potential within year variation in weight-length parameters is expected among

TABLE 3.—Estimated von Bertalanffy growth parameters for Atlantic menhaden, year classes 1955-78.

Year class	L_∞	K	t_0	n (means)	Age range (years)
1955[1]	339.49	0.5401	0.1234	7	0-7
1956	343.67	0.4598	0.0245	7	0-8
1957	324.49	0.6260	0.0707	7	0-7
1958	363.73	0.3637	−0.1163	7	0-7
1959	355.64	0.3631	−0.4709	6	0-6
1960	354.69	0.4009	−0.1481	5	0-5
1961	340.52	0.4514	−0.3506	5	0-5
1962	376.35	0.4012	−0.1122	5	0-5
1963	370.04	0.3494	−0.4652	6	0-6
1964	331.17	0.6138	0.0606	5	0-5
1965[2]	404.13	0.3187	−0.3529	17	0-6
1966	367.15	0.4575	−0.0645	18	0-6
1967	375.81	0.4539	0.1815	16	0-5
1968	415.22	0.2813	−0.7318	16	0-5
1969	356.19	0.5868	0.0530	18	0-6
1970	348.00	0.5351	0.0034	16	0-5
1971	356.82	0.4103	−0.2772	18	0-6
1972	316.74	0.6058	0.0767	17	0-5
1973	341.53	0.3884	−0.2947	20	0-5
1974	325.60	0.4329	−0.1280	22	0-6
1975	420.86	0.1779	−1.1445	21	0-6
1976	393.73	0.2410	−0.4372	20	0-5
1977	528.99	0.1455	−0.8354	16	0-4
1978	246.54	0.5807	−0.3399	12	0-3

[1]Year classes 1955-64 represented by fitted values for 4th quarter, area 5 (see text).
[2]Year classes 1965-78 represented by fitted values for weighted quarterly mean lengths.

quarters. Because each area (except perhaps area 5) contains a limited portion of the range of sizes extant in the menhaden population, the weight-length relationship is estimated across areas, but within quarters. Annual variation was also assumed to exist, thus parameter estimates were calculated for each fishing season where subsequent yield-per-recruit analysis was intended (1970-78) using $\log_e$ transformed data and least squares regression (Table 4).

Annual Mean Weights Weighted by Catch

Estimates of annual weighted mean weight by age of Atlantic menhaden in purse seine catches were calculated to permit computations of age-specific and year class-specific biomass contributions to landings. Weighted mean weight for the entire fishery was calculated from the average weight by age by season for each of the five recognized areas of the fishery and then weighted by the estimated numbers caught by age in each respective area. These data were derived directly from the port sampling data and are not from von Bertalanffy derived lengths converted to weights.

VIRTUAL POPULATION ANALYSIS

Virtual population analyses (VPA's) were conducted to reconstruct population sizes and estimate rates of fishing mortality. Analyses were conducted on all age groups of the 1947-78 year classes which were represented in the 1955-81 landings. The backward sequential computations were performed using the computer program MURPHY written by Tomlinson (1970).

Instantaneous Rate of Natural Mortality

The estimate of the annual instantaneous rate of natural mortality (M) used in this report was 0.45. Early estimates were from catch statistics, 0.37 (Schaaf and Huntsman 1972); from preliminary tag-recovery analysis, 0.52 (Dryfoos et al. 1973); and from a more extensive tag-recovery analysis, 0.50 (mean of age-specific rates for ages 2 and 3) (Reish et al. 1985). The 0.45 value represents a mean of the range of available estimates. The implications of the selection of 0.45 for M are addressed.

Temporal Organization of Analyses

The time periods used in these analyses (Table 2) closely correspond to critical life history and fishery events. The birth date for a year class, and the beginning of a new fishing season for Atlantic menhaden, is 1 March. Because of the protracted spawning season of menhaden, young of the year may have been spawned as early as the previous August and as late as the following May or June, but most of the spawning takes place in the fall and winter (Nelson et al. 1977). The beginning of the fourth quarter (week beginning ≥ Nov. 29) is used as a finite date to estimate spawning stock size. Thus, the spawning stock in the fall (beginning of the fourth quarter) of the previous calendar year (age X.75) is defined to be the parental stock for a subsequent (1 March) year class. Recruitment is examined at age 0.5 (beginning of third quarter, age 0) and at age 1.0 (beginning of first quarter, age 1).

Three sets of VPA's were conducted with the length of the time intervals varied between sets. The first set provided the basic estimates for reconstruction of the historical population and the estimates of rates of fishing mortality. This series was done on an annual basis and involved all subject year classes. These estimates are used pri-

TABLE 4.—Weight-length regression parameters for Atlantic menhaden, by quarter and year, 1970-81 seasons ($\ln W = a + b \ln L$).

Fishing years	Quarter 1		Quarter 2		Quarter 3		Quarter 4		Annual	
	a	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*
1970	−11.9324	3.1924	−11.5760	3.1224	−11.3909	3.0971	−11.5124	3.1087	−11.6666	3.1421
1971	−10.8692	2.9838	−11.0121	3.0135	−11.4336	3.0941	−12.0821	3.2044	−11.3620	3.0786
1972	−13.0384	3.3809	−11.5388	3.1072	−11.5989	3.1131	−11.5413	3.1028	−11.6553	3.1264
1973	—	—	−10.6360	2.9401	−10.7756	2.9741	−11.4291	3.0889	−10.9727	3.0060
1974	−12.8892	3.3503	−11.3321	3.0695	−11.2386	3.0552	−12.1803	3.2310	−11.4423	3.0896
1975	−10.3727	2.9027	−11.9798	3.1950	−11.7856	3.1555	−11.6995	3.1388	−11.8524	3.1703
1976	−10.9908	2.9972	−12.5123	3.2945	−12.4698	3.2933	−11.9663	3.1873	−12.3503	3.2642
1977	−12.6133	3.3110	−12.9689	3.3856	−11.9884	3.2043	−12.0643	3.2109	−12.5865	3.3137
1978	−12.3304	3.2666	−12.5737	3.3096	−12.0319	3.2124	−11.8477	3.1642	−12.3324	3.2653
1979	−11.9230	3.1950	−11.8170	3.1701	−12.0982	3.2243	−12.5516	3.2900	−12.4043	3.2793
1980	−12.2804	3.2580	−12.8763	3.3696	−11.9109	3.1884	−11.7750	3.1547	−12.3969	3.2792
1981	−12.2049	3.2386	−12.4031	3.2765	−12.6597	3.3215	−11.9663	3.1747	−12.5365	3.3004

marily in discussions of the impact of nominal effort and for modification of input variables for surplus production analysis.

The second series, with shorter time intervals, permitted a more precise apportioning of fishing mortality between fishing areas within a fishing season and provided within season estimates of numbers at age present in the population. This series was conducted on a quarterly basis and included the 1965-78 year classes. These estimates permitted a reconstruction of the fishery for the 1970-78 seasons which forms the basis of the subsequent yield-per-recruit analyses. The quarterly estimates of numbers at age are also used to estimate numbers of recruits for the 1965-78 year classes and the numbers of spawners that were ultimately derived from these year classes.

The third series was conducted to estimate numbers of recruits and their parental spawning stock for the 1955-64 fishing seasons. This series included the 1947-64 year classes and used mixed length time intervals. A 1/2-yr interval, which included ages 0.50 and 0.75 (quarters 3 and 4), was used to provide estimates of numbers of age-0.5 individuals present in the population. The time interval for age-1 fish was annual. Intervals for age-2 and older individuals were alternately three quarters of a year (quarters 1-3), corresponding to ages X.0-X.50, and one quarter of a year (quarter 4), corresponding to age X.75. This temporal construction of the numbers at age data required several adjustments which are discussed.

Additional VPA's were conducted to examine the sensitivity of results to the value of natural mortality used (0.45) and to the initial estimates of fishing mortality rates. A series of annual VPA's were conducted for the 1955-78 year classes with $M = 0.35$ and $M = 0.55$, which encompass the range of available estimates discussed earlier. Additional annual runs were conducted with varied starting F's for the 1955 year class, which for reasons discussed later, potentially represents a worst case situation relative to rates of convergence of estimates.

VPA Numbers at Age Landed Data Sets

The annual estimates of numbers at age caught were rearranged from a seasonal format to a year-class format. For the quarterly runs, the weekly catch at age estimates were summed to quarters and rearranged by year class. The mixed time interval VPA data sets were derived from the annual set, and thus required some approximations and adjustments to obtain a subyear format. Annual catches of age 0 (1955-64 seasons) were assumed to be in quarters 3 and 4 since the bulk of the age-0 catches occurred after 30 August (beginning of the third quarter). The major portion, if not all, of the catches of age-2+ fish (spawning ages) that were made during the fourth quarter time interval, was in the North Carolina fall fishery. During the 1965-69 fishing seasons, an average of 58% of the age-2+ fish that were landed in the fall fishery were landed during the fourth quarter. Hence, 58% of the fall fishery landings of age-2+ fish of the 1947-64 year classes were assumed to have been taken during the fourth quarter. The remainder of the total annual catch was assigned to the single three-quarter time interval (quarters 1-3). The time period used for the age-1 fish remained annual, so no adjustments were required.

Estimates of Initial Annual Rate of Instantaneous Fishing Mortality

Although a single method of estimation for the starting instantaneous annual fishing mortality rate (F) for backward calculations in VPA is desirable, a few year classes required alternate approaches. Year class-specific catch curves were examined visually. All years of age from the oldest to youngest that lie within a reasonably straight portion of a semilogarithmic catch plot were $\log_e$ transformed and regressed against age. The slope was taken as an estimate of $-Z$ (total instantaneous mortality) and by subtracting M a "general trend" F was obtained. Starting F's were obtained by this method for all year classes except 1947, 1948, 1949, 1954, 1966, 1971, 1974, and 1978. Since only 2 years of landings after full recruitment were available for the 1978 year class, an estimate of Z was made: $-\log_e$ (catch in numbers of age 3/catch in numbers of age 2). The estimate for 1949 was obtained similarly using ages 7 and 8. The 1954, 1966, 1971, and 1974 year classes experienced an apparently higher fishing rate during their last year in the fishery compared with that experienced 1 year earlier. Thus, starting F's were obtained from average VPA results from several other age classes caught in the same year. Starting F for age 8 of the 1954 year class was estimated as the mean F for ages 5-7 (year classes 1955-57) caught in the same 1962 season. Initial F for age 5 of the 1966 year class was the annual VPA estimate of age 4 from the 1967 year class. Similarly, starting values of F for the 1971 and 1974 year classes were the means of the same fishing season age-4 and age-5 values for the 1972 and 1973, and 1975 and 1976 year classes. Starting F's on age 8 for the 1947 (one age class represented) and 1948 (two age classes represented) year classes were means of similar fishing season VPA F's for ages 5-7. The initial annual F values and their sources for VPA are summarized in Table 5.

Conducting the VPA computations for the annual series was straight forward, as the trial F's were annual. The quarterly series and mixed time interval series required trial and error runs. Trial starting F's for these VPA's were adjusted downward until the sum of the F's within the last year (oldest fish of the year classes) were $\pm 0.5\%$ of the initial annual F estimate for each year class (Table 5).

Except for the sensitivity computations, the general results of the VPA's are presented and discussed where they are subsequently used. Using a relatively wide range of starting values for the 1955 year class, estimates of age-specific F and numbers at age present at the beginning of a season (Fig. 7) converged quite rapidly to similar values for the (younger) ages which dominate the fishery in both numbers and biomass (Figs. 8, 9). This is expected because of the relatively high rates of fishing mortality exerted on the stock (Ulltang 1977). The lower the exploitation rate, the slower the values will converge. The 1955 year class had the lowest starting F of any year class (Table 5) (other than 1947 which had only one age class represented) and relatively low to moderate rates of exploitation on all age classes. Thus the estimates for the other year classes should converge more rapidly than the one shown. Since it is highly unlikely that the initial estimates of F differ from true values to the extreme degrees tested, the VPA estimates used

TABLE 5.—Estimates of initial F for annual virtual population analyses (VPA's) of Atlantic menhaden, source of estimate, and ages involved, by year class.

Year class	Initial F	VPA's ages	Regression ages	Mean from VPA results[1]
1947	0.4862	8	—	yes
1948	1.3134	7-8	—	yes
1949	1.3498[1]	6-8	—	—
1950	1.6504	5-8	6-8	—
1951	0.9243	4-8	4-8	—
1952	0.8590	3-8	5-8	—
1953	0.8620	2-8	2-8	—
1954	1.1645	1-8	—	yes
1955	0.7006	0-8	2-8	—
1956	0.8557	0-8	2-8	—
1957	1.0651	0-8	5-8	—
1958	1.8497	0-8	4-8	—
1959	1.4325	0-7	3-7	—
1960	1.7620	0-6	2-6	—
1961	3.0108	0-6	4-6	—
1962	1.9074	0-6	2-6	—
1963	2.0482	0-6	2-6	—
1964	2.1116	0-5	2-5	—
1965	2.7386	0-5	3-5	—
1966	1.6194	0-5	—	yes
1967	1.1191	0-5	2-5	—
1968	1.6677	0-5	2-5	—
1969	1.9585	0-6	3-6	—
1970	2.2554	0-5	2-5	—
1971	1.5437	0-6	—	yes
1972	1.7143	0-5	2-5	—
1973	1.5403	0-5	2-5	—
1974	1.4321	0-6	—	yes
1975	1.3185	0-6	2-6	—
1976	1.0167	0-5	2-5	—
1977	1.3079	0-4	2-4	—
1978	1.4391	0-3	—	—

[1]See text.

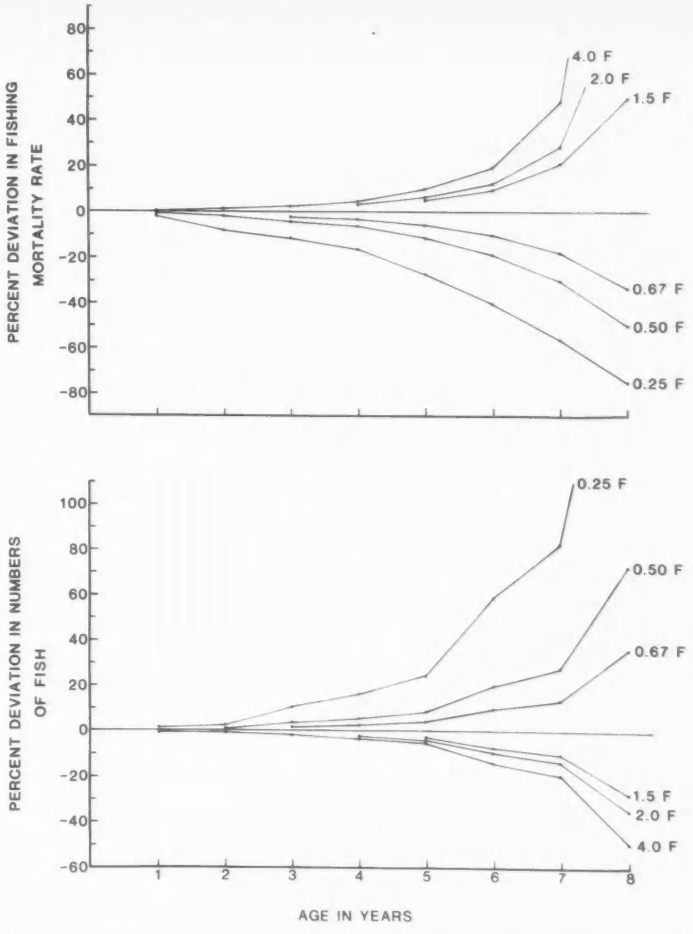

FIGURE 7.—Deviations in annual VPA (virtual population analysis) estimates of numbers at age present in the population and age specific fishing mortality rates for Atlantic menhaden resulting by varying the initial rate of annual F by the multiples shown. The estimates are for the 1955 year class (initial F = 0.7006).

here should be considered reasonably precise (and stable) relative to the initial F values.

Since F and M are additive with respect to Z, errors in these computations resulting from an incorrect selection of the rate of M are additive with respect to subsequent estimates of F, and estimates of numbers at age present in the population will differ in a proportional fashion. In other words, if our selection of the estimate of M is too great, numbers at age are overestimated, and if M is too low, the reverse is true (Fig. 10). Similarly, estimates of year class size vary by a nearly constant proportion (Fig. 11). The range of available estimates of M is relatively narrow, hence it is unlikely that conclusions reached in this report would be altered even if the estimate of M for these analyses were allowed to vary randomly within these bounds between years.

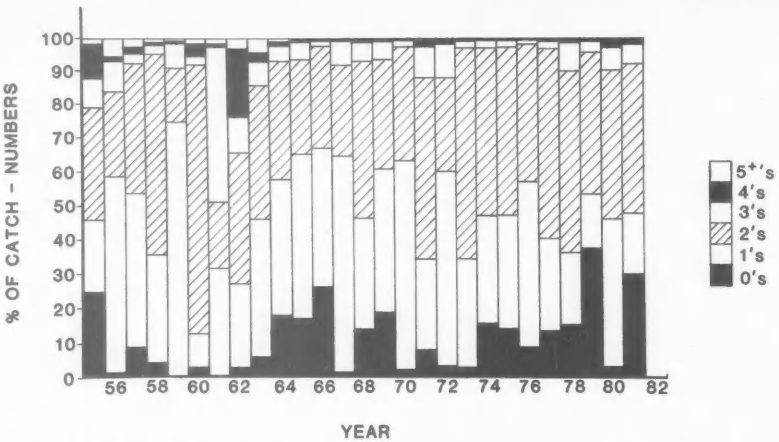

FIGURE 8.—Contribution in percent of total numbers of Atlantic menhaden landed by age group, from 1955 to 1981.

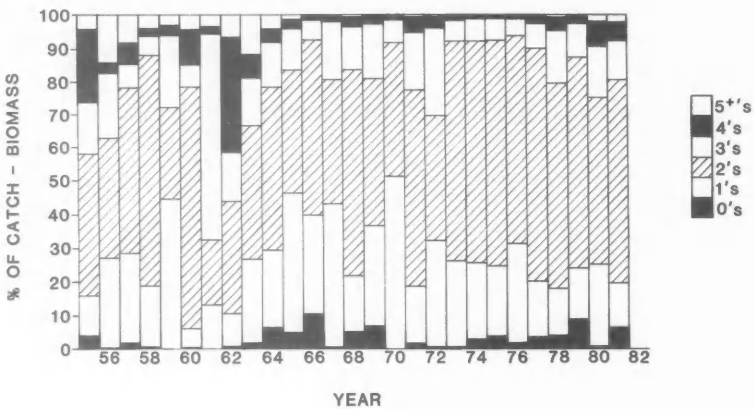

FIGURE 9.—Contribution in percent of total biomass of Atlantic menhaden landed by age group, from 1955 to 1981.

SPAWNER-RECRUITMENT RELATIONSHIP

Estimates of Numbers of Spawners

Higham and Nicholson (1964) concluded that a few age-1 Atlantic menhaden and most age-2 fish are sexually mature by the end of the season. The simplifying assumption for purposes of estimating spawning stock in these analyses is that no age-1 fish and all age-2 fish are mature by the beginning of the fourth quarter. This assumption was also used in other studies (Nelson et al. 1977; ASMFC fn. 4; Schaaf and Huntsman 1972).

Estimates of the number of fish age 2.75 and greater alive at the beginning of the fourth quarter of any given year n comprised the parental spawning stock for year class $n + 1$. The estimates of number of spawners resulting from the 1947-64 year classes were obtained from the mixed time-interval VPA series. The number of spawners from the 1965-78 year classes were ob-

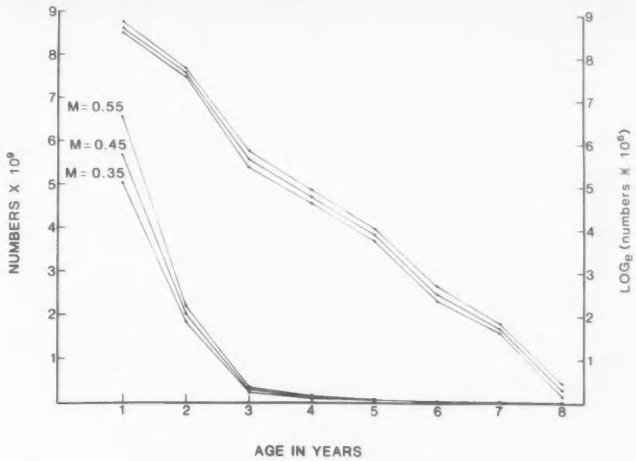

FIGURE 10.—VPA (virtual population analysis) estimates of numbers at age present in the Atlantic menhaden population for the 1955 year class for three levels of natural mortality (lower left), and natural logarithms of these same numbers at age (upper right).

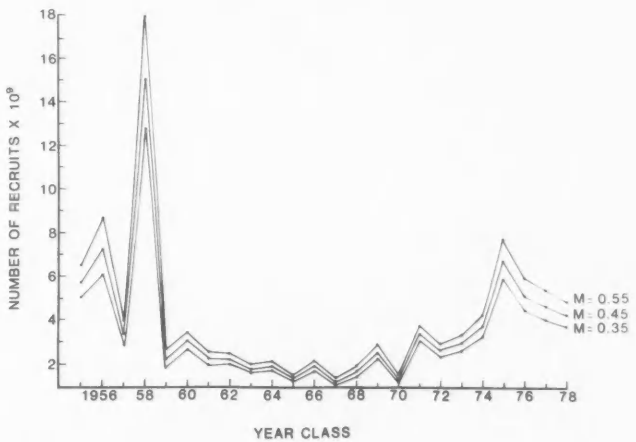

FIGURE 11.—Annual VPA (virtual population analysis) estimates of numbers of Atlantic menhaden recruits at age 1 for three levels of natural mortality.

tained from the quarterly VPA series. These estimates were rearranged to correspond to fishing seasons (Table 6). There were no estimates for numbers at age landed in the 1954 North Carolina fall fishery. Hence, the parental spawning stock for the 1955 year class was obtained by using 1955 estimates for age X.0 and back-calculating numbers at age to the beginning of the 1954 fourth quarter (age (X − 1).75) with mean fourth quarter survival rates at age for fishing years 1955-57. An additional adjustment was made to complete the estimates of spawning stock size. If an age group was represented during quarters 1-3 but not in quarter 4 of the last year it

TABLE 6.—Estimates of spawning stock size in thousands by age for Atlantic menhaden, 1954-81 seasons, at start of the fourth quarter of each fishing season.

	Age						
Year	2.75	3.75	4.75	5.75	6.75	7.75	8.75+
1954[1]	720,068.8	966,532.5	158,421.1	44,416.7	10,592.6	2,383.0	NE
1955	750,253.7	216,441.3	325,276.2	50,554.4	12,061.1	3,463.6	932.1
1956	285,976.8	213,151.0	102,272.1	98,950.9	11,254.9	2,541.6	593.9
1957	321,399.1	99,134.2	72,526.3	35,097.5	19,882.5	1,250.7	362.0
1958	1,060,499.7	145,248.4	46,161.4	29,036.6	11,021.2	5,504.1	82.2
1959	330,845.0	366,056.3	65,942.6	19,506.9	7,873.1	2,094.9	1,339.2
1960	2,662,230.0	144,140.8	125,048.6	20,387.2	5,552.2	1,337.9	693.7
1961	432,466.5	736,311.5	69,834.8	46,372.7	6,667.1	1,300.3	144.1
1962	215,894.3	84,439.3	97,991.5	18,987.4	6,579.9	1,795.1	258.7
1963	173,757.5	43,433.2	17,968.5	15,709.5	2,756.5	991.8	539.0
1964	151,149.8	26,764.3	4,358.7	2,199.5	1,112.9	157.6	194.2
1965	101,340.2	12,848.1	1,419.3	164.1	180.0	53.7	13.2
1966	194,222.2	18,780.6	1,401.8	15.5	18.0	27.4	5.4
1967	133,362.5	36,015.8	2,858.6	207.1	0.5	0	0
1968	122,033.7	16,235.3	1,227.0	199.0	8.1	0	0
1969	125,131.1	26,492.8	761.0	16.4	1.1	0	0
1970	175,837.2	34,303.4	6,017.2	48.1	0	0	0
1971	265,058.8	29,169.5	4,107.8	619.4	0	0	0
1972	64,386.9	14,863.7	1,187.3	766.8	0	0	0
1973	80,116.3	5,210.6	2,021.8	142.9	0	0	0
1974	94,348.3	7,760.3	241.5	153.0	0	0	0
1975	140,817.4	12,947.3	356.3	12.9	13.8	0	0
1976	212,735.5	37,466.2	2,306.5	164.1	0	0	0
1977	498,135.8	59,415.2	5,630.1	245.6	22.3	0	0
1978	451,889.2	80,962.9	13,390.0	927.6	0	0	0
1979	486,903.4	155,932.5	26,789.6	2,772.6	47.3	0	0
1980	424,606.5	103,707.0	42,254.5	4,995.9	909.8	0	0
1981	-No. est.-	57,691.0	14,868.6	7,335.7	397.5	0	0

[1]Derived from 1 March 1955 estimates (see text).

appeared in the fishery, it was assumed that some representatives were still present in the population at the beginning of quarter 4 (age X.75). Estimates of numbers present were obtained by a forward calculation using the mortality estimates of the previous interval obtained from the VPA's.

Estimates of Potential Egg Production

The age structure of the Atlantic menhaden population varied substantially during the time period under study. Therefore, an alternate method of examining spawning stock (i.e., potential egg production) as used by Nelson et al. (1977) was employed.

Sizes at age X.75 for spawners derived from the 1955-78 year classes were calculated from the von Bertalanffy growth parameters derived earlier for the entire fishery (Table 3). However, because of insufficient data, growth curves were not fitted to the 1947-54 year classes, so observed mean lengths at age during the fourth quarter were used for the spawners derived from these year classes. If the fourth quarter length at age was not available, means from the nearest three year classes were used.

Estimates of egg production were obtained from the expression used by Nelson et al. (1977), which was derived from data of Higham and Nicholson (1964):

$$\ln(E) = 0.3149 + 0.0176L$$

where, E = thousands of eggs produced per female, and
L = estimated fork length.

This equation was used with estimated mean length at age X.75 for fish 2 years and older. Assuming a 50/50 sex ratio, potential egg production by age by season was obtained by multiplying the values per female by number of females at age (Table 7).

Estimates of Numbers of Recruits

Estimates of the number of recruits for each year class were obtained from the results of the VPA's. The year class-size estimates for 1955-64 are from the mixed time-interval analyses and

TABLE 7.—Estimated number of recruits by year class at age 0.5 and 1.0, estimated number of spawners that produced the year class, and estimated egg production from the spawning stock, for Atlantic menhaden.

Year class	Number of recruits × 10^3		No. of spawners × 10^3	No. of eggs × 10^{12}
	Age 0.5	Age 1.0		
1955	7,888,342	5,621,258	1,902,414.7	219.659
1956	8,999,656	7,153,549	1,358,982.4	147.047
1957	4,419,989	3,263,196	714,741.2	83.977
1958	18,612,316	14,767,294	549,652.3	57.768
1959	2,722,999	2,164,428	1,297,553.6	143.822
1960	3,786,692	2,958,923	793,658.0	76.642
1961	2,769,147	2,210,534	2,959,390.4	156.058
1962	2,841,268	2,222,880	1,293,097.0	106.781
1963	2,304,564	1,754,140	425,946.2	37.508
1964	2,764,796	1,938,001	255,156.0	21.466
1965	2,072,852	1,430,539	185,937.0	13.806
1966	2,879,544	2,001,871	116,018.6	7.552
1967	1,522,438	1,209,954	214,470.9	17.017
1968	2,319,215	1,710,666	172,444.5	13.053
1969	3,448,326	2,611,940	139,703.1	11.240
1970	1,755,217	1,382,032	152,402.4	12.056
1971	4,513,962	3,539,073	216,205.9	17.594
1972	3,516,016	2,760,443	298,955.5	31.279
1973	3,908,494	3,085,954	81,204.7	8.044
1974	5,197,484	3,866,593	87,491.6	6.076
1975	9,024,340	6,932,136	102,503.1	6.591
1976	6,953,329	5,297,439	156,147.7	7.575
1977	6,619,024	4,827,413	252,672.3	11.966
1978	6,040,678	4,404,267	563,449.0	18.864
1979[1]	10,322,177	6,890,589	547,169.7	18.389
1980	NE	NE	672,445.4	26.045
1981	NE	NE	576,473.7	22.294

[1]Preliminary estimates.

those for 1965-78 are from the quarterly analyses. Estimates of recruitment were computed for both age 1.0 and age 0.5 (Table 7). Estimates at age 1.0 are provided for comparative purposes, as this age has been frequently used for studies on Atlantic menhaden (ASMFC fn. 4). Age 0.5 is used here to appropriately credit a year class with the numbers of juvenile fish removed from the population by the fishery during the fall and early winter. Although perhaps underestimates because the value of M (0.45) may be too low for fish younger than 1-yr old, these estimates are relatively consistent.

The degree of dependency of the number of recruits on the size of the parental stock has been examined by Schaaf and Huntsman (1972), Nelson et al. (1977), Schaaf (1979), and Reish et al. (1985). All earlier workers employed the Ricker (1954) model, but Reish et al. (1985) also used the Beverton and Holt model as well as the unnormalized gamma function. The published results indicate weak relationships, with substantial variability about both fitted models. Nelson et al. (1977) developed a multiple regression model to explain observed deviations from the Ricker model attributable to several annually varying environmental parameters, primarily Ekman transport, which would affect the oceanic larval stage.

The spawner-recruitment data (Table 7) were fitted with both the Ricker and Beverton-Holt models using a nonlinear least squares method (Marquardt's (1963) algorithm). Both models fit the data poorly (Fig. 12). The Beverton-Holt model is slightly better than the Ricker model if residual sum of squares is used as a goodness of fit criterion. The Beverton-Holt residual is only slightly less than that about a mean value, which assumes no relationship between numbers of spawners and numbers of recruits. Residual sum of squares in the Ricker model was slightly greater than results for the mean.

POTENTIAL AND ACTUAL YIELD

Production Models

The application of production models to the Atlantic menhaden purse seine fishery is hampered on theoretical grounds by two major conditions: 1) the fishery has not been operating under equilibrium conditions, and 2) fishing effort is not proportional to fishing mortality (F). The catchability coefficient (q) is inversely related to population size (Schaaf 1975b). Schaaf and Huntsman (1972) and Schaaf (1979) circumvented this latter problem by adjusting effort to a base year.

The effects of this problem were reduced in this analysis by using an estimate of population F for the independent variable instead of adjusting effort (Nelson and Ahrenholz 1986). To estimate a population rate of fishing mortality (F_{pop}), estimates of the population sizes (excluding 0-age fish) at the beginning of each fishing season from 1955 to 1979 were reconstructed from annual VPA estimates. These were in turn divided into the estimated catch in numbers (excluding age 0), to obtain an estimate of population rate of exploitation (U_{pop}). By trial and error, estimates of F_{pop} were obtained for each fishing season from $F_{pop} = U_{pop} Z/(1 - e^{-Z})$, assuming $M = 0.45$ (Table 8).

A Graham-Schaefer curve was fitted to the catch and population fishing mortality data by Marquardt's (1963) algorithm. This procedure produced an MSY (maximum sustainable yield) estimate of 414,000 t at $F_{pop} = 0.574$. Recent population fishing mortality values have been slightly above and below this value, and yield has

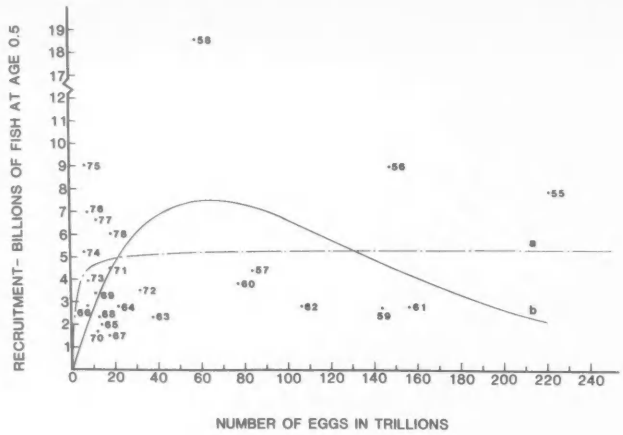

FIGURE 12.—Numbers of Atlantic menhaden recruits (R) in millions plotted against estimated egg production (P) in trillions for year classes 1955-1978. Curve a represents the fitted Beverton and Holt function, R = 1/(0.00019 + 0.00027/P). Curve b represents the fitted Ricker function, R = 325.35 P exp (−0.0158 P).

TABLE 8.—Estimates of Atlantic menhaden population size and catch in numbers in thousands (age 1 to maximum observed age), population exploitation rates, population *F*, and catch in thousands of metric tons, by year.

Year	Population size	Catch in numbers	Population exploit. rate (*U*)	Population *F*	Catch (t)
1955	6,955,987.3	2,357,430.0	0.3389	0.532	641.4
1956	8,305,282.6	3,528,450.0	0.4248	0.721	712.1
1957	9,829,843.1	3,212,090.0	0.3268	0.508	602.8
1958	7,125,101.7	2,613,150.0	0.3668	0.590	510.0
1959	17,630,370.1	5,342,240.0	0.3030	0.462	659.1
1960	9,309,904.0	2,702,940.0	0.2903	0.438	529.8
1961	6,843,711.6	2,598,060.0	0.3796	0.618	575.9
1962	4,587,482.6	2,048,280.0	0.4465	0.774	537.7
1963	3,602,666.4	1,667,620.0	0.4629	0.816	346.9
1964	2,770,398.2	1,426,470.0	0.5149	0.961	269.2
1965	2,593,453.3	1,260,362.0	0.4860	0.878	273.4
1966	2,127,951.0	991,157.0	0.4658	0.824	219.6
1967	2,592,784.2	977,255.0	0.3769	0.612	193.5
1968	2,098,231.9	993,717.0	0.4736	0.845	234.8
1969	2,281,471.7	710,048.0	0.3112	0.478	161.6
1970	3,507,601.0	1,379,039.0	0.3932	0.648	259.4
1971	2,555,012.9	896,250.0	0.3508	0.556	250.3
1972	4,466,635.5	1,664,286.0	0.3726	0.602	365.9
1973	4,294,409.0	1,780,916.0	0.4147	0.697	346.9
1974	4,433,007.7	1,671,675.0	0.3771	0.612	292.2
1975	5,401,009.0	1,857,415.0	0.3439	0.542	250.2
1976	8,927,821.9	3,005,106.0	0.3366	0.527	340.5
1977	8,652,084.7	3,181,191.0	0.3677	0.592	341.2
1978	7,855,446.4	2,622,620.0	0.3339	0.522	344.1
1979	7,370,472.2	2,353,757.0	0.3193	0.493	375.7

remained slightly below the MSY value (Fig. 13).

Catch and F_{pop} values were also fitted to a modified version of the Pella-Tomlinson (1969) model, which compensates for nonequilibrium conditions (PRODFIT)(Fox 1975), assuming two significant year classes. This technique resulted in an MSY estimate of 557,000 t at $F_{pop} = 0.336$ (Fig. 13).

The scatter plot of yield/F_{pop} contains three

clusters of yield values: high abundance gears (1955-62), low abundance (high F_{pop}) years of 1963-68 (with the exception of 1967), and years of low to moderate population size (1969-79). These clusters are less distinct when yield is measured in numbers of fish rather than biomass. A Graham-Schaefer curve, fitted to fishing mortality and yield in numbers of fish, resulted in a numbers MSY of 2.383 billion fish at an optimum $F_{pop} = 0.522$ (Fig. 14). Each year's yield in numbers as compared to biomass (Fig. 13, 14) suggests that the fishery in the late 1970's was not produc-

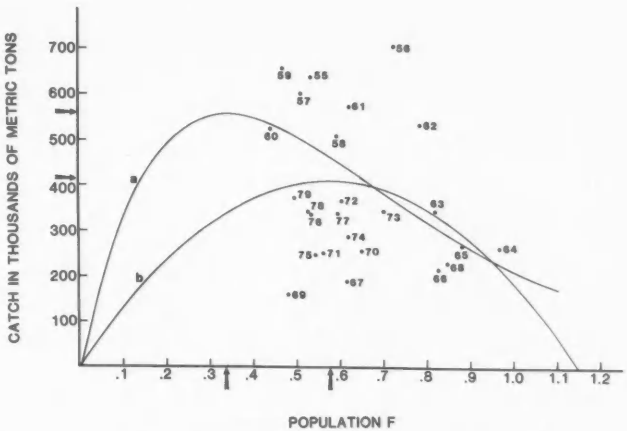

FIGURE 13.—Catch of Atlantic menhaden in thousands of metric tons plotted against estimates of population F for years 1955-79. Curve a is the result of fitting the Pella-Tomlinson's (1969) generalized yield function with adjustments for nonequilibrium conditions (PRODFIT, Fox (1975)). Curve b is a nonlinear least squares fit of the parabolic (Graham-Schaefer) production model.

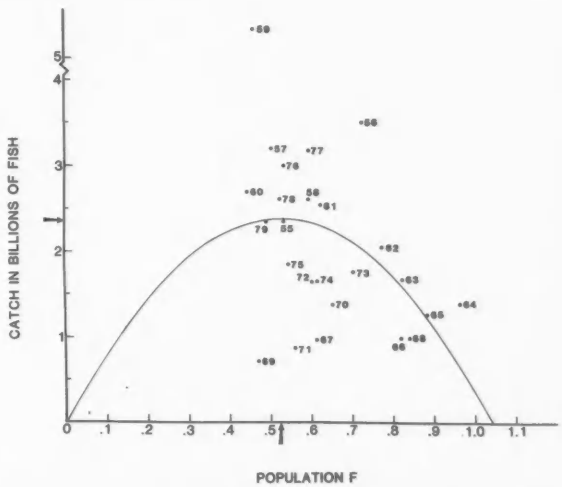

FIGURE 14.—Catch of Atlantic menhaden in billions of fish against estimates of population F for years 1955-79. The curve is the result of a nonlinear least squares fit of the parabolic (Graham-Schaefer) production model.

ing the biomass in landings in proportion to numbers of fish caught when compared to earlier years.

Catchability coefficients (q_{pop}) for the population were estimated directly by dividing the F_{pop} estimates by nominal effort (vessel weeks) for years 1955-79. A plot of these estimates on population size indicates a pronounced inverse relationship similar to that shown by Schaaf (1975b), who estimated q differently (Fig. 15). Additionally, there is a pronounced historical trend in the data. There appear to be at least two families of points and thus two functional curves in the figure, 1955-69 and 1970-79. Beginning in 1959, the catchability coefficient progressively increased, the stock size was decreasing, and the fleet was becoming more efficient due to modernization and increased vessel size, coupled with technological innovations in the fishery operations themselves. This trend in efficiency probably made the ascent from the earlier, lower q_{pop} series of years exceptionally rapid. As population size began to increase after 1971, the catchability coefficient reflected a steady decline in magnitude, but it was at a level almost twice as great (hence a doubling in killing power or efficiency[7]) as from the late 1950's and early 1960's. Therefore, the reduction in the number of vessels from 1955 to the present did not represent a proportional reduction in potential effective fishing effort. In spite of the compounding effect of a true increase in efficiency (fishing technology), q, and thus F for given levels of effort, appear to be responding in inverse fashion to population size.

The computed F_{pop} values are derived independently of nominal effort. Hence this set of values was used to determine if effort would be useful to verify trends in F at age or provide supportive information for improving the VPA estimates by employing more sophisticated models (see Deriso et al. 1985). A scatter diagram of the differences between estimates of F_{pop} and their mean on nominal effort demonstrated that no useful information is available from nominal effort when considering the entire time span involved (Fig. 16). The progressive increase in efficiency of the purse seine fleet, plus problems associated with estimating abundance with CPUE data from purse seine fisheries for schooling fishes (see Clark and Mangel 1979) makes nominal effort useful only for relatively short-time span comparisons between adjacent years, and then only when changes are pronounced.

Yield Per Recruit

Yield-per-recruit calculations for the 1970-78 fishing seasons were performed using the com-

[7]Given modern day work weeks, real time spent fishing, and intervessel competition, the killing power has probably more than doubled.

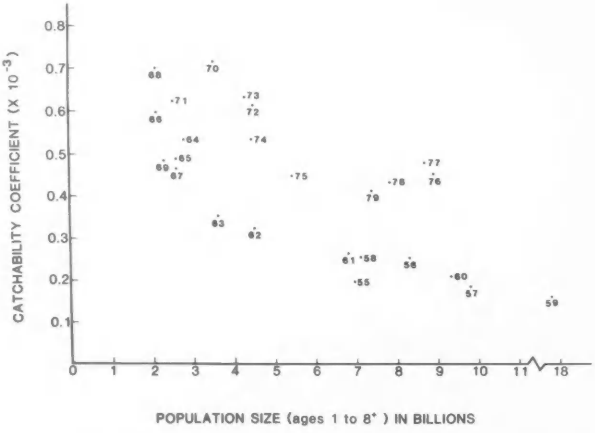

FIGURE 15.—Estimates of the Atlantic menhaden population catchability coefficient (q_{pop}) for years 1955-79, plotted against the estimated population size (excluding age-0 fish).

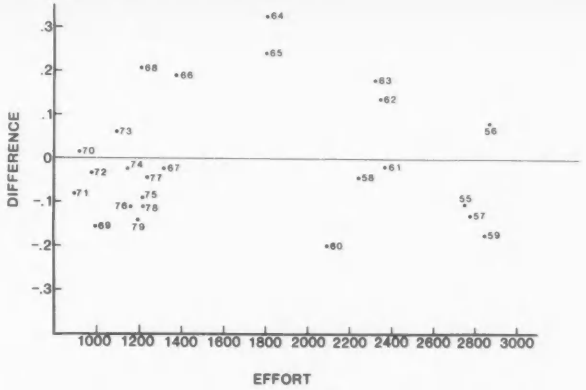

FIGURE 16.—Differences between observed Atlantic menhaden population fishing mortality rates (F_{pop}) and their mean plotted against nominal effort by fishing season.

puter program MAREA (Epperly et al. 1986) assuming exponential growth of the biomass in the population (Epperly and Nelson 1984). This program, modified for Atlantic menhaden from MGEAR (Lenarz et al. 1974), uses the Ricker-type yield-per-recruit model (Ricker 1975) and permits estimation of yield in each of the Atlantic menhaden fishing areas, with area-specific growth and fishing mortality rates. Each computer run of the model generates a matrix of yield per recruit at varied age of entry and multiples of F for each of the fishing areas (5) and one for the entire fishery. Yield for the entire fishery can be obtained either by summing yield from each area or by calculations based on input from the entire fishery estimated as a unit. A summation of the five matricies should be similar (but not equal) to the independently calculated entire fishery matrix. Input for the model includes estimates of area specific proportional fishing mortalities, estimates of weight at age by area and for the entire fishery, and an estimate of M (0.45).

Estimates of area-specific quarterly F at age were obtained by apportioning F at age for the entire fishery (obtained from the quarterly VPA, 1965-78 year classes) with the ratios of the number at age caught in a given area to the total number at age landed in the entire fishery. (The resulting proportional F's are not equivalent to true area specific F's, but are the correct values for the yield-per-recruit model used).

Area-specific length at age estimates for the beginning of each quarter for each year class were rearranged to correspond to fishing season, and converted to weight at age using season-specific weight-length equations (from Table 4). Parallel conversions were done on lengths at age for the entire fishery to estimate weights at age for the fishery as a whole.

Annual trends in historic yield per recruit were examined with the fishing mortality, age and size, and geographic pattern extant during each year from 1970 to 1978. Results from these computations indicate a severe decline in actual yield per recruit for the entire fishery and Chesapeake Bay area from 1971 to 1978 (Fig. 17).

Estimates of potential changes in yield per recruit under regimes of varied age at entry and (multiple) changes in fishing mortality rate were obtained by averaging parameters reflecting conditions during 3-yr intervals, i.e., 1970-72, 1973-75, and 1976-78 (Table 9). Attainment of the maximum potential yield from Atlantic menhaden in the purse seine fishery would have required a very high rate of fishing at a substantially delayed age at entry of about 3 years of age (Figs. 18, 19). More practically, yield could have been increased by reducing F's. For example, with a F multiplier of 0.6 and the current age of entry, the gain would have been 6.9% for the conditions of 1976-78 (Fig. 19, Table 9). With an increase in age of entry to 1.0 (eliminate the harvest of age-0 fish) the gain would have been 10.2%. The patterns of potential gain for conditions under the 1970-72 and 1973-75 time periods are similar, but of lesser magnitude (Fig. 18, Table 9).

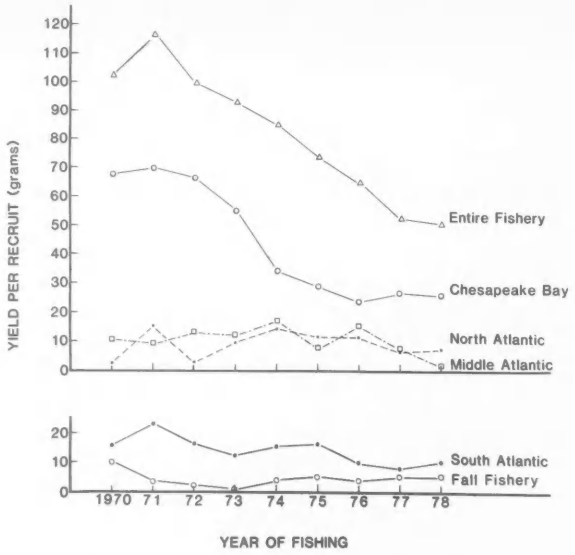

FIGURE 17.—Estimated yield per recruit of Atlantic menhaden for fishing patterns and growth prevalent during years 1970-78.

TABLE 9.—Estimates of percentage change in yield per recruit of Atlantic menhaden with varied age at entry and rates of *F* for 1970-72, 1973-75, and 1976-78. The *F* multiple of 1.0 represents the *F* at age vector extant during each of the three time periods.

Time period	Age at entry	*F* - multiple						
		0.4	0.6	0.8	1.0	1.2	1.4	1.6
1970-72	4.0	−35.8	−23.3	−16.1	−11.8	−9.2	−7.5	−6.3
	3.5	−21.9	−8.9	−1.7	2.6	5.3	7.3	8.7
	3.0	−12.7	0.2	6.2	9.8	12.0	13.4	14.4
	2.5	−4.6	6.8	12.1	14.9	16.5	17.5	18.1
	2.0	0.5	9.9	13.6	15.1	15.8	16.0	16.0
	1.5	−0.7	7.0	9.3	9.6	9.1	8.3	7.3
	1.0	−3.4	2.1	2.6	1.3	−0.6	−2.6	−4.7
	0.5	−3.9	1.4	1.5	(107.33)[1]	−2.1	−4.3	−6.5
1973-75	4.0	−7.7	4.6	10.5	13.6	15.4	16.5	17.3
	3.5	1.1	12.5	17.7	20.4	22.1	23.1	23.8
	3.0	10.5	20.2	24.2	26.2	27.3	27.9	28.4
	2.5	13.3	19.4	20.9	21.1	20.8	20.4	19.9
	2.0	12.8	15.2	14.8	14.0	13.2	12.5	12.0
	1.5	10.3	11.2	9.6	7.8	6.0	4.5	3.1
	1.0	8.2	8.1	5.6	2.9	0.5	−1.7	−3.7
	0.5	6.9	6.2	3.1	(84.07)[1]	−2.9	−5.5	−7.9
1976-78	4.0	−5.9	12.7	23.5	30.0	34.1	36.8	38.8
	3.5	1.5	18.8	27.8	32.7	35.5	37.1	38.1
	3.0	9.8	25.6	33.2	37.0	39.0	40.0	40.7
	2.5	12.1	22.7	26.0	26.5	26.0	25.1	24.2
	2.0	11.7	17.8	18.2	17.0	15.6	14.3	13.2
	1.5	9.6	14.0	13.2	11.0	8.8	6.7	4.9
	1.0	7.2	10.2	8.3	5.2	2.1	−0.7	−3.2
	0.5	5.0	6.9	3.9	(56.84)[1]	−3.8	−7.2	−10.3

[1]Estimated yield per recruit in grams for conditions of the time period, which is the base value for calculation of percentage change.

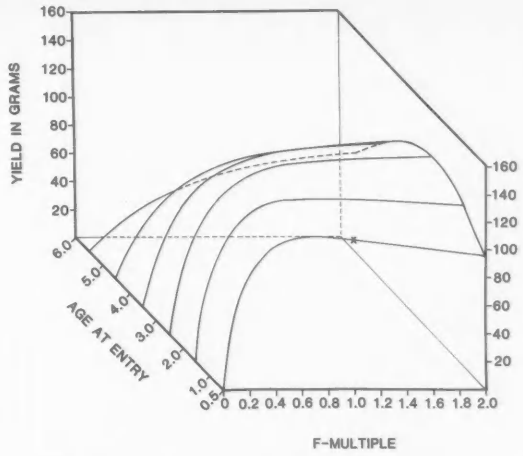

FIGURE 18.—Hypersurface representation of potential yield per recruit for Atlantic menhaden with varied age of recruitment and fishing mortality for conditions extant during 1970-72. The X denotes estimate of actual yield per recruit for the time period.

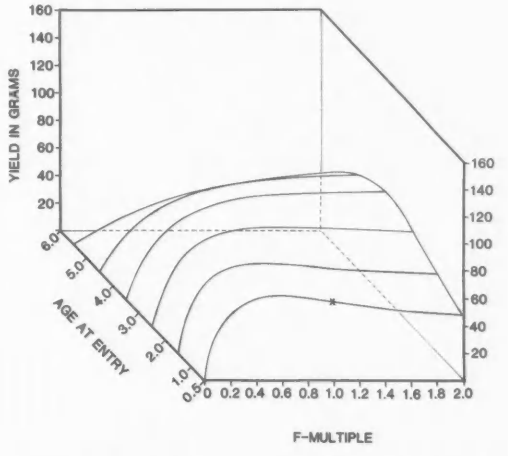

FIGURE 19.—Hypersurface representation of potential yield per recruit for Atlantic menhaden with varied age of recruitment and fishing mortality for fishing conditions extant during 1976-78. The X denotes estimate of actual yield per recruit for the time period.

Results from these analyses indicate a general reduction in the maximum potential as well as actual yield per recruit from the early to the late 1970's, but the maximum potential total yield is greater in the later time period due to increased numbers of recruits (Table 10). Thus, estimation of potential changes in yield by the Atlantic menhaden fishery from yield-per-recruit models becomes a function of density-dependent growth rates (lower yield per recruit with larger year

TABLE 10.—Estimates of yield per recruit (grams) and mean yield (thousands of metric tons) of Atlantic menhaden for three, 3-yr intervals, maximum possible yield per recruit (Y/R) and yield with the existing fishing pattern.

Years	Mean no. of recruits $\times 10^6$	Estimated Y/R (g)	Mean yield estimate (t)	Maximum Y/R (g)	Maximum yield (t)	Increase %
1970-72	2,711.8	107.33	291.1	127.56	345.9	18.8
1973-75	3,778.2	84.07	317.6	108.40	409.6	29.0
1976-78	6,340.5	56.84	360.4	80.49	510.3	41.6

classes), rate of fishing, geographical pattern of fishing, age of recruitment, and numbers of recruits.

The general conclusion reached with these analyses is that the stock suffers from growth overfishing. To determine if a different initial choice of a constant rate of M would alter this conclusion, the relative biomass of a hypothetical year class was estimated at specific ages with M equal to 0.35, 0.45, and 0.55 and F equal to zero. The growth equation for the 1970 year class (from Table 3) and the annual weight-length expression for 1972 (from Table 4) were used in these computations. The age of maximum biomass decreases with increasing rates of M, as expected, but even at $M = 0.55$ the age of maximum biomass exceeds 2.5 years (Fig. 20). This decrease (from about age 2.8 for $M = 0.45$) is insufficient to affect the conclusion of growth overfishing. However, if the initial choice of M is too high, the analyses are underestimating potential gains in total yield that could be realized by decreasing fishing pressure on younger ages. Similarly, if the choice of M is too low, the analyses are overestimating potential gains, but a net gain would still be realized within the range of available estimates of M.

Actual Yield by Year Class

Using the estimates of numbers caught by age and annual weighted mean weights at age, annual landings were apportioned into biomass at age landed and then summed by year class through age 5. The calculations provide estimates of yield by each year class. A plot of yield against year-class size reveals lower than expected yields from the 1975 and 1976 year classes, given their magnitude (Fig. 21). This trend appears to have started about 1973.

Comparisons of growth and mortality patterns were made of similar-sized year classes, 1955 and 1976, and 1956 and 1975, in search of causes of the observed decrease in yield. Differences in fishing mortality rates at age do not explicitly account for the dramatic differences in yield between the two pairs of similar-sized year classes (Table 11). The 1955 year class was harvested at a greater (less desirable) rate during the critical

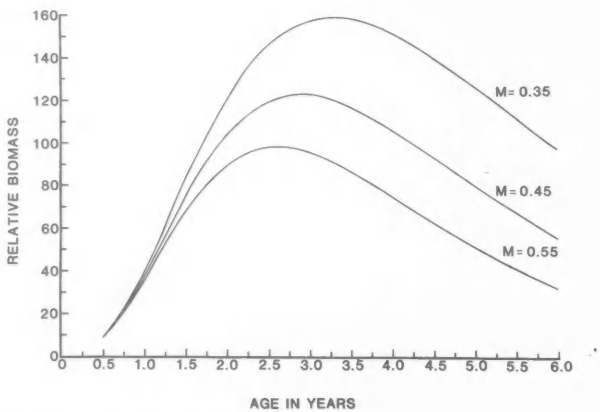

FIGURE 20.—Age-specific relative biomass estimates of a hypothetical year class of Atlantic menhaden in the absence of fishing, exposed to three rates of natural mortality. If the year class was harvested instantaneously at any given age, the corresponding ordinate value would represent yield per recruit in grams.

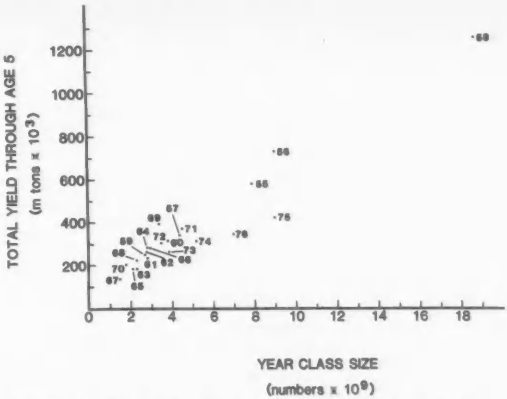

FIGURE 21.—Estimated yield contribution of Atlantic menhaden in thousands of metric tons, by the 1955-76 year classes through age 5, plotted against year class size.

TABLE 11.—Estimates of annual F at age for the 1955 and 1976, and 1956 and 1975 year classes of Atlantic menhaden, through age 5.

Year class	Age					
	0	1	2	3	4	5
1955	0.10	0.58	1.56	0.39	0.43	0.90
1976	0.04	0.27	1.51	0.57	1.04	1.02
1956	<0.01	0.32	0.88	0.74	0.61	0.48
1975	0.03	0.34	1.60	1.48	0.60	1.82

ages of 0-2 than was the 1976 year class. In fact, yield from the 1955 year class could have been markedly increased with a reduced fishing rate on these younger fish. The harvest rates of the 1956 and 1975 year classes were similar for ages 0-1, but markedly greater at age 2 for the 1975 cohort. While the high age-2 fishing mortality rate probably contributed to the lower yield, it did not fully explain the marked difference. The generally higher rates of F for ages 3-5 exhibited for both the 1975 and 1976 year classes were probably inconsequential for this comparison of yield.

While an increase in the true value of natural mortality could cause a decrease in total yield by year class, differences in growth provide a more obvious explanation for the differences within these two pairs of year classes. Growth curves (in length and weight) for the 1956 and 1975 year classes and the 1955 and 1976 year classes show that individuals were much smaller during the dominant harvest ages (1-3) for the two most recent year classes (Figs. 22, 23). These differences could be great enough to account for most of the differences observed in yield. Slower relative growth in post age-1 fish has been apparent for year classes 1973-78.

To determine if age of maximum theoretical biomass had changed owing to the different (flatter) shaped growth curves displayed by the year classes in the later 1970's, the relative biomass at age of an unfished hypothetical year class was estimated with the growth equation for the 1975 year class with M equal to 0.45 and the annual weight-length expression for 1972. The results display an increase in maximum age (to about 3.25 years), a decrease in total biomass, and a much slower ascent and even slower descent from maximum biomass than results for the 1970 year class growth curve (Fig. 24). These results indicate that age of entry to the fishery could have been greatly delayed in the later 1970's with little chance of losing yield.

Given the progressive decrease in average size at age of fish in the age classes which dominate landings (Fig. 25), the decline in yield per recruit following 1971 (Fig. 17) is expected. However, the rapid decline in size at age is not entirely ascribable to density-dependent growth. More importantly, the potential for increased yield with reductions in F is probably greater than the results from the MAREA yield-per-recruit model indicate owing to the likelihood of size selective fishing and the potential for differential stock-specific growth rates. Additionally, the relatively high MSY estimate obtained from the PRODFIT

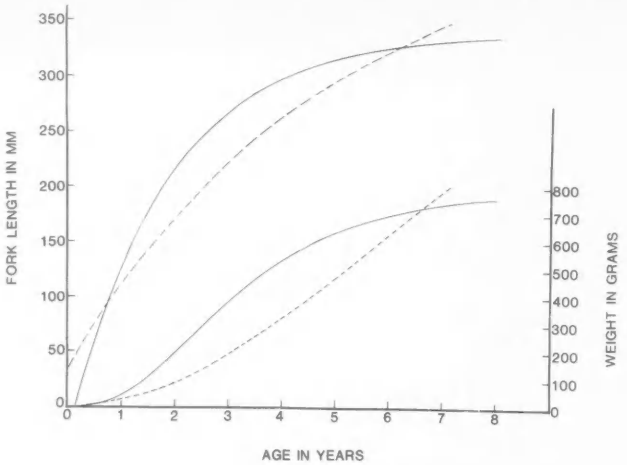

FIGURE 22.—Comparative fitted von Bertalanffy growth curves of two similar-sized (numbers of fish) Atlantic menhaden year classes, 1955 (solid curves) and 1976 (dashed curves). Upper curves are fork length in millimeters, and lower curves are weight in grams.

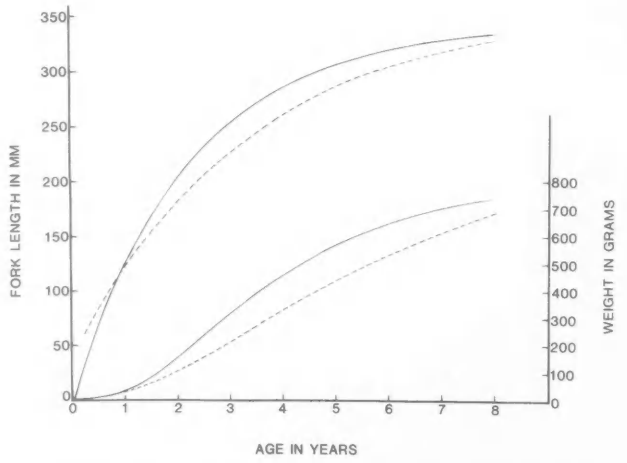

FIGURE 23.—Comparative fitted von Bertalanffy growth curves of two similar-sized (numbers of fish) Atlantic menhaden year classes, 1956 (solid curves) and 1975 (dashed curves). Upper curves are fork length in millimeters, and lower curves are weight in grams.

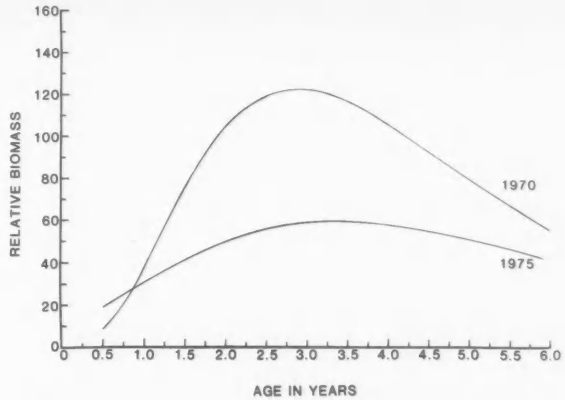

FIGURE 24.—Age-specific relative biomass estimates of a hypothetical year class of Atlantic menhaden in the absence of fishing, with growth parameters estimated for the 1970 and 1975 year classes. If harvesting occurred instantaneously at any given age, the corresponding ordinate value would represent yield per recruit in grams.

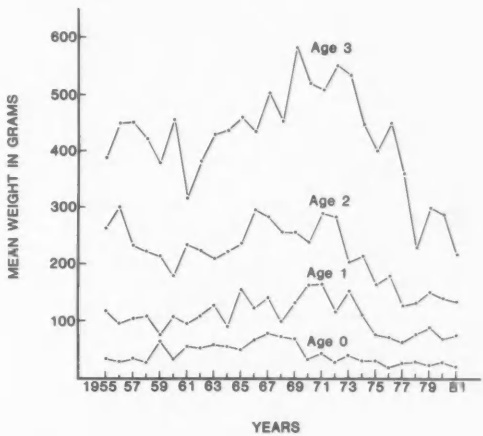

FIGURE 25.—Weighted mean annual weight of purse seine landed Atlantic menhaden, ages 0-3, for years 1955-81.

solution shown earlier may be more realistic than first impressions would indicate. However, to attain that level of harvest would require a restructuring of the fishery, and continued moderate to high levels of recruitment to sustain it.

GENERAL DISCUSSION

With estimates of year-class sizes, exploitation rates, and an understanding of the interaction of population size and effort relative to rates of fishing mortality, the trends observed in the fishery since 1955 are more readily explained. Additionally, this information permits inferences to be drawn about the earlier presampling period of the 1940's and early 1950's. The major premise of this discussion is that harvest levels and effort of the earlier presampling period were probably near

the maximum that the population could support, and thus the rather rapid growth of the fishery in the early to mid-1950's was a response to a substantial increase in abundance of Atlantic menhaden and not simply increased effort applied to an underexploited stock.

Changes in stock abundance due to fluctuations in spawning success were prevalent in the 1940's. This conclusion is drawn from the statement of purpose for study given by June and Reintjes (1959). They noted changes in abundance among geographic areas and seasons and some poor catches. This condition is expected when recruitment fluctuates in a fishery that has a stock which is differentially distributed by age and size.

Data from early years indicated a limited resource. Catch closely paralleled effort for the 1941-47 seasons, but catches during 1948 and 1949 (about 350,000 t) were less than expected given the effort expended (Fig. 1). Apparently the stock subsequently underwent a marked increase in abundance, noticeable first about 1952, but even more pronounced in 1953 and 1954. The fishery responded, as effort again began to rise, but lagged for the next two or three seasons. In 1959 catches were dominated by the 1958 year class, which continued to provide significant biomass to the fishery through 1962.

It appears that the 1950's marked a period with above average recruitment, and this was accentuated with the apparently very large 1951 year class, followed by the three relatively large year classes of 1953, 1955, and 1956, and finally the largest documented year class of 1958. Recruitment did not return to the level of the 1955 year class (the lesser of the three documented large year classes) until 1975. To obtain some idea of relative sizes, a reconstruction of these earlier year classes was made using arbitrary, but conservative values for F (F = 0.25 for age 1 and 0.50 for age 2+) (Table 12). Given the (older) larger sized fish which were taken during the peak landing years, these speculative year class estimates are less than or nearly equal to a size necessary to support the large catches of the mid-1950's (see Figure 14 and Table 7).

The age structure of the Atlantic menhaden population has undergone at least two periods of expansion and contraction since about 1950, and has shown signs of expanding again by 1980 (Fig. 6). Inferences on early age composition were derived primarily from the early 1952-54 sampling of the fishery in the middle Atlantic area (June and Reintjes 1959, their appendix table 2). Age-5 and older fish were 1.0%, 0.8%, and 1.1% by number in the samples from that area for 1952, 1953, and 1954 as compared to 1.8% and 2.9% for 1955 and 1956. The 1951 year class dominated the catch during this period, comprising 84.59% of the samples as age 1, 98.05% as age 2, and 59.02% as age 3 in the middle Atlantic area and 87.11% as age 3 in the newly sampled north Atlantic area. Hence, as noted earlier, the stock probably had its strongest age structure in 1955 and 1956, which were coincidentally the first years for which port sampling covered the full geographic range of the fishery. This strength was due to the increased population size, subsequent decrease in the catchability coefficient, and thus a reduced fishing mortality on most age groups. Higher rates of survival led to more individuals in the older age groups. The landings were sustained above 500,000 t in the mid-1950's by contributions of the 1955 and 1956 year classes, but these year classes were too small to prevent an increase in mortality because of increased effort and the number of older fish were reduced by 1959. The large 1958 year class aided the replenishment of the older age groups, by about 1960. Without another large year class,

TABLE 12.—Estimates from virtual population analyses (mixed time interval, see text) of number at age in thousands on 1 March for the 1950-59 year classes of Atlantic menhaden. Bracketed values represent estimates obtained from back calculations using arbitrary values of F (0.25 for age 1 and 0.50 for ages 2+)

Age	Year class									
	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
1	[3,943,235]	[10,782,529]	[3,162,907]	[4,504,191]	3,040,558	5,621,258	7,153,549	3,263,196	14,767,294	2,164,428
2	[1,958,152]	[5,354,445]	[1,570,653]	2,236,715	1,410,646	1,976,767	3,306,709	1,412,179	6,627,079	1,158,337
3	[757,298]	[2,070,784]	607,436	642,482	240,748	274,476	893,865	275,897	2,357,641	361,743
4	[292,878]	800,857	189,410	169,952	80,038	119,036	270,347	116,411	602,146	71,280
5	113,268	281,543	86,255	53,482	37,304	48,835	92,494	59,258	75,460	11,589
6	43,677	63,025	23,309	21,243	14,284	12,269	35,962	14,698	8,894	1,616
7	5,980	11,726	7,639	3,717	2,765	5,618	4,883	1,629	901	161
[1]8	600	3,564	1,446	478	1,162	1,331	640	92	48	—

[1]This age group may contain a small number of age 9 or 10 individuals, see text.

mortality apparently again increased, as the age structure became markedly constricted by 1965, and drastically truncated by 1967. Recruitment began to improve by 1971, culminating with relatively large year classes in 1975 and 1979. Mortality rates for some ages began to decline during the late 1970's, and the older age groups began to strengthen, consistent with the decline of the catchability coefficient with increased population size.

With respect to yield per recruit, there appears to be no recorded period of Atlantic menhaden fishing when an ideal harvesting regime existed in the purse seine fishery. Age-0 fish have been harvested since at least 1955 (Figs. 8, 9). Except for influences of the exceptionally large 1951 and 1958 year classes, most of the catches sampled for age have been dominated by age 2 relative to biomass, and ages 1 and 2 relative to numbers. Major numerical but minor biomass contributions have been evident for age-0 fish. Inferences of the fishery's high dependency on younger age groups can be traced back to 1940. Given that the population distributes itself by age and size along the Atlantic coast, the quantity of landings and degree of effort expended in areas where younger and smaller fish predominate suggests a similar age composition for total catches during the presampling period (Figs. 3, 5).

Landings in the middle Atlantic area dominated the fishery in earlier years, but a shift had occurred by 1964, at which time Chesapeake Bay landings began to dominate (Fig. 4). Responding to a reduced population of larger and older fish, the industry increased the proportion of fishing effort exerted in areas closer to the large nursery areas of Chesapeake Bay and the south Atlantic area. Further, the fishery shifted from one that harvested the larger age 1's and 2's, and older fish, to one that harvests the smaller and younger fish. The larger, older fish were and still are vulnerable to the fishery during their fall migrations, but effort on these fish appears to be reduced within the north Atlantic and middle Atlantic areas.

A comparison of age-specific estimates of exploitation rates supports the earlier discussion on age dependency, population sizes, and age structure (Fig. 26). In the mid-1950's, the exploitation rates, although varying, were lower than those

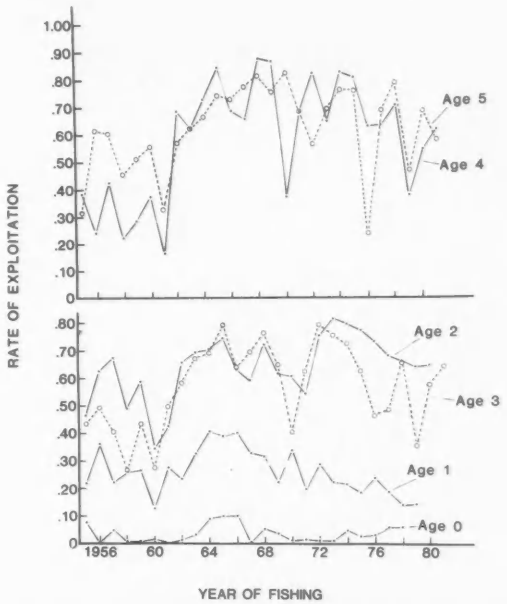

FIGURE 26.—Estimates of annual rates of exploitation of Atlantic menhaden, ages 0 through 5.

for the subsequent years when population size was decreasing. The rates reached their lowest points for ages 1-3 during 1960, when the 1958 year class was fully recruited. A low point followed for ages 4 and 5 during 1961. All exploitation rates generally increased during the low recruitment years of the 1960's, and began decreasing during the 1970's as the population size began to increase due to higher recruitment. The rate of reduction noted for nominal effort (Fig. 1) lagged behind that of the stock and was apparently too slow to prevent the observed rise in exploitation rates during the 1960's.

The exploitation rates of age-2 fish appear to have progressively declined during the later 1970's, following a disproportionately large increase after 1971. This increase apparently was a product of a shift in the pattern of fishing that occurred during the regrowth of the fishery and that pattern still exists. Although slightly lagging behind that of the age-2 fish, exploitation rates on age-0 fish began increasing by 1974, and reached an alarming rate of about 15% in 1979 (preliminary estimate). This rate of exploitation occurred in virtually one quarter of fishing and slightly exceeded the rate of exploitation for age-1 fish for the entire season. The disproportionately low exploitation rate on age 1's is probably due to their increasingly smaller size, a consequence of which would be a more southerly distribution. Additionally, many would remain in or near estuarine nursery areas and surrounding smaller bays and sounds, and thus be less available to the fishery.

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DENSITY AND DEPTH DISTRIBUTION OF LARVAL GULF MENHADEN, *BREVOORTIA PATRONUS*, ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*, AND SPOT, *LEIOSTOMUS XANTHURUS*, IN THE NORTHERN GULF OF MEXICO

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ABSTRACT

Densities of larval gulf menhaden, *Brevoortia patronus;* Atlantic croaker, *Micropogonias undulatus;* and spot, *Leiostomus xanthurus*, compared among three transects in the northern Gulf of Mexico, indicated that all three species were more abundant at inshore (18 m isobath) than offshore stations (91 and 183 m isobaths). Gulf menhaden and Atlantic croaker were most abundant off Southwest Pass, Louisiana, a major outlet of the Mississippi River into the Gulf of Mexico. Gulf menhaden larvae caught at inshore stations were larger than those collected at offshore stations. Of the three species, only gulf menhaden showed any consistent pattern in vertical distribution. At inshore stations, gulf menhaden were concentrated near the surface at midday, but distributed across sampling depths (1 m, 6 m, and 12 m) at dawn, dusk, and midnight, a pattern opposite to that typically reported for larval fish. At offshore stations (with sampling depths of 1 m, 30 m, and 70 m), gulf menhaden larvae were present at 70 m, but most were caught near the surface. A concentration in surface waters was again most pronounced at midday.

Gulf menhaden, *Brevoortia patronus;* spot, *Leiostomus xanthurus;* and Atlantic croaker, *Micropogonias undulatus*, are thought to spawn offshore in winter months in the northern Gulf of Mexico (Nelson 1969; Fore 1970; Diaz 1982; Christmas et al. 1982). Larvae of the three species are transported inshore to nursery grounds in marshes and estuaries along the northern coast. One passive mechanism suggested for movement of gulf menhaden includes longshore advective transport, entrainment into the coastal boundary layer, and eventual transport into the estuary effected by the seasonal rise of sea level in spring (Shaw et al. 1985a). The passage of winter cold fronts can also be expected to influence transport.

Spawning of gulf menhaden occurs in shelf waters out to at least 91 m (Guillory et al. 1983), but is concentrated around the Mississippi River Delta (Fore 1970). Atlantic croaker apparently spawn in waters <54 m in depth (Diaz 1982), while spot spawn in waters >27 m (Dawson 1958; Nelson 1969). Gulf menhaden larvae spend 3 to 5 weeks at sea before entering estuaries when they are 12 to 25 mm in length (Reintjes 1970; Christmas and Etzold 1977; Guillory et al. 1983).

Fish larvae are nonrandom in their spatial distribution in both the vertical and horizontal dimensions. One primary influence on the vertical distribution of larvae is their diel vertical movement (migration) in the water column; larvae of many species rise to the surface by night and descend by day (e.g., Smith et al. 1978; Kendall and Naplin 1981; Sameoto 1982, 1984). Horizontal distribution is also dynamic, with dispersion and aggregation of larvae affected by such factors as adult spawning behavior, water mass movements, localized larval mortality, and larval behavior (Smith 1981; Houde 1982; Jahn and Lavenberg 1986).

In this study we examined the density and depth distribution of larval gulf menhaden, spot, and Atlantic croaker at three locations in the northern Gulf of Mexico, with emphasis on the area around Southwest Pass, LA, the main discharge of the Mississippi River among the delta distributaries. Size distributions of gulf menhaden were compared to determine if inshore larvae were older than offshore larvae, the expected pattern if adults are spawning primarily offshore and larvae are moving inshore.

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METHODS

Larvae were collected along three inshore-offshore transects (off Southwest Pass, LA; Cape San Blas, FL; and Galveston, TX) at stations positioned over the 18 m (10 fm), 91 m (50 fm), and 183 m (100 fm) isobaths (Fig. 1). Sampling took place on four cruises in December 1979, February 1980, December 1980, and February 1981. Collections were made with a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS, Wiebe et al. 1976). The MOCNESS consisted of nine 505 μm mesh Nitex[3] plankton nets with mouth openings of 1 m by 1.4 m. Due to equipment problems, only the inshore Southwest Pass station was sampled on the first cruise. Galveston stations were added to the sampling program on the February 1981 cruise.

MOCNESS nets were deployed in the following manner: Net 1 remained open as the MOCNESS descended from the surface to the deepest depth to be sampled. Nets 2 and 3 sampled at that depth, one at a time, and net 4 opened as the MOCNESS was raised to an intermediate depth, where nets 5 and 6 sampled. Net 7 was open while the MOCNESS was brought to the surface, where nets 8 and 9 fished. Discrete depth nets generally fished from 2 to 3 minutes before deployment of the next net. Sampling depths were approximately 12, 6, and 1 m at inshore stations and 70, 30, and 1 m at the offshore stations. At each station, MOCNESS casts were made at 0600, 1200, 1800, and 2400 h, with a towing speed of approximately 2 nmi/hour. Sensors on the MOCNESS provided continuous recording of temperature and depth. Two flowmeters, one mounted on top of the MOCNESS and one within the net opening, were used to calculate the volume of water sampled by each net and to detect net clogging. The mean volume filtered by each discrete depth net was 140 m^3 (SD = 101.2, n = 529).

The collection of one net at each discrete depth was preserved in 5% buffered formalin-seawater and the collection of the other was preserved in 70% ethanol. Formalin-preserved larvae were used in gut content analysis (Govoni et al. 1983), and alcohol-preserved larvae were used in otolith analysis of age and growth (Warlen in prep[4]). In the laboratory all fish larvae were removed from

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]S. M. Warlen. Manuscr. in prep. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

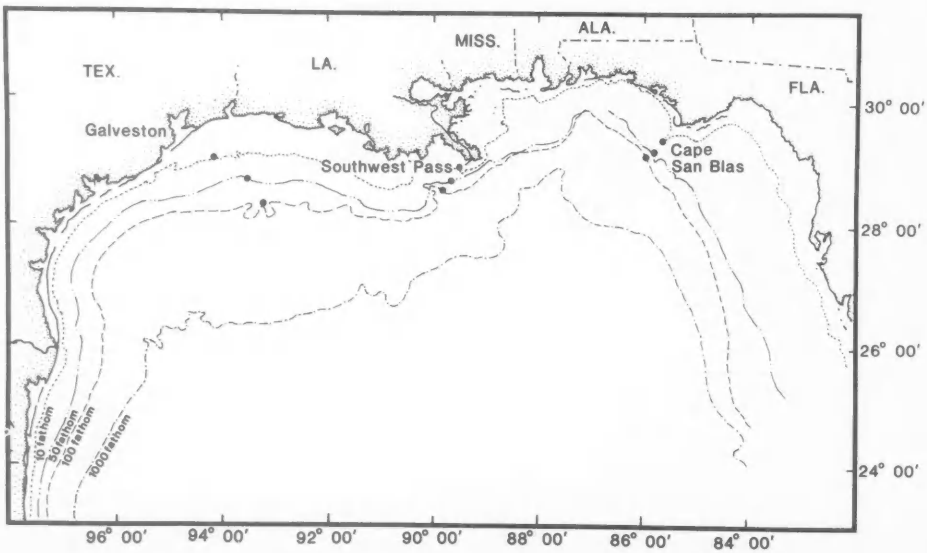

FIGURE 1.—Location of sampling transects and stations in the northern Gulf of Mexico.

the samples and counted. Gulf menhaden were measured (standard or notochord length) to the nearest 0.01 mm with an ocular micrometer. When more than 30 menhaden occurred in a sample, 30 individuals were randomly selected and measured (length measurements were not corrected for shrinkage). Due to the scarcity of larvae at outer stations, menhaden from both the 91 and 183 m Southwest Pass stations were combined in the comparison of offshore size distribution with inshore (restricted to the Southwest Pass station to allow valid comparison). Spot and Atlantic croaker were too rare at all offshore stations to allow size comparisons.

Analysis of vertical movement was based on the mean percentage of larvae caught at each of three discrete depths on each MOCNESS cast, allowing comparison among casts with widely varying densities of larvae. Gulf menhaden caught at the inshore stations were divided into three size classes to determine if vertical distribution varied with age. Because of the low number of larvae at the 183 m stations (see above), analysis of offshore vertical distribution was based on MOCNESS casts from both the 91 and 183 m stations. Mean densities at each depth were also calculated for each time of sampling.

RESULTS

Overall densities (number $\times$ 100 m^{-3}) of gulf menhaden, spot, Atlantic croaker, and the total of all species (these three species plus all others, including damaged and unidentifiable clupeids that may have been gulf menhaden) varied widely among cruises, stations, times, and depths. The majority of the 529 net tows did not catch any gulf menhaden (67%), spot (83%), or Atlantic croaker (82%). Smaller individuals of all three species, however, were probably not retained by the 505 μm mesh nets. In all but four cases, gulf menhaden were more abundant than spot or Atlantic croaker (Table 1). The density of all three species was generally greatest at the inshore (18 m) stations and declined offshore, with low or zero densities common at both offshore stations of Cape San Blas and Galveston (Table 1).

Gulf menhaden were most abundant at the Southwest Pass stations, except on the December 1980 cruise, when they were most abundant at the 18 m Cape San Blas station (Table 1). Atlantic croaker larvae were most abundant at the inshore Southwest Pass station in December 1980 and February 1981, but not in February 1980. Spot

TABLE 1.—Mean densities (SD in parentheses) of ichthyoplankton (larvae $\times$ 100 m^{-3}) collected at three stations at three sites in the northern Gulf of Mexico. Densities are averaged over three discrete depths and four times of day. Station 1 was over the 18 m isobath, station 2 over the 91 m isobath, and station 3 over the 183 m isobath. *n* = number of net tows. "Total larvae" includes the three target species and all others.

Cruise	Station	*n*	Total larvae	Gulf menhaden	Spot	Atlantic croaker
Dec. 1979	SW Pass 1	24	78.5 (88.9)	43.7 (66.9)	1.3 (2.3)	3.5 (3.9)
Feb. 1980	SW Pass 1	24	228.7 (281.4)	79.3 (122.5)	1.1 (0.3)	0.1 (0.3)
	SW Pass 2	23	32.1 (43.0)	7.4 (16.0)	0	0
	SW Pass 3	7	7.5 (5.9)	0.4 (0.7)	0	0
	San Blas 1	24	20.0 (14.4)	0.2 (10.5)	0.6 (0.9)	0.6 (0.8)
	San Blas 2	23	114.3 (85.3)	0.1 (0.2)	0.1 (0.3)	0.1 (0.4)
	San Blas 3	16	18.4 (13.2)	0	0	0
Dec. 1980	SW Pass 1	35	38.4 (30.4)	6.0 (8.0)	0.1 (0.2)	9.1 (15.2)
	SW Pass 2	24	56.0 (55.5)	8.8 (18.3)	0.2 (0.6)	3.1 (7.8)
	SW Pass 3	24	43.7 (38.4)	0.7 (2.1)	0	0
	San Blas 1	24	330.5 (618.6)	14.1 (42.4)	98.1 (259.3)	0.1 (0.1)
	San Blas 2	24	112.8 (83.2)	0	0.5 (1.2)	0.1 (0.3)
	San Blas 3	24	55.1 (61.0)	0	0	0
Feb. 1981	SW Pass 1	23	36.7 (49.7)	26.8 (43.8)	0.6 (0.9)	1.8 (2.6)
	SW Pass 2	22	65.8 (69.1)	13.6 (17.5)	0.6 (0.9)	0.6 (1.2)
	SW Pass 3	24	18.6 (15.0)	6.2 (11.8)	0.1 (0.1)	0
	San Blas 1	23	28.7 (15.8)	0	0	0
	San Blas 2	24	10.0 (9.0)	0	0	0
	San Blas 3	24	9.3 (6.8)	0	0	0
	Galveston 1	23	53.2 (26.1)	9.3 (6.8)	0	0
	Galveston 2	24	87.1 (65.0)	0.1 (0.1)	0	0
	Galveston 3	24	22.1 (16.4)	0	0	0

larvae were never very abundant except at the inshore San Blas station on the December 1980 cruise (Table 1), when a single dense patch of larvae was encountered on two successive MOCNESS casts (Govoni et al. 1985). Densities were as high as 993 larvae × 100 m^{-3}, an abundance not observed for other species and not approached by spot densities in any other sample. On the February 1981 cruise, no spot larvae were collected at this station. The occurrence of this aggregation, then, appeared to be a reflection of patchiness rather than geography.

An inshore-offshore comparison (Southwest Pass stations) of menhaden lengths revealed that on two of three cruises (February 1980 and December 1980) larvae were larger at the inshore station (Table 2). This was not the case on the third cruise, however, when mean lengths were similar. Results of a two-way ANOVA (Table 2) indicated significant differences in mean length for both main effects of station and cruise and for their interaction ($P < 0.001$). Thus, the pattern to the data is more complex than can be summarized by main effects alone. Length-frequency distributions indicated a bimodal pattern at the inshore station with most larvae in the larger size mode (Fig. 2). Larger larvae were not as common at the offshore stations except on the final cruise, when a bimodal pattern occurred offshore as well as inshore.

At the inshore stations, total larvae were generally distributed evenly among the three sampling depths at all times of day (Fig. 3), although

TABLE 2.—Mean standard length (mm, SE in parentheses) of gulf menhaden caught on three cruises at inshore (18 m isobath) and combined offshore (91 and 183 m isobaths) stations off Southwest Pass, LA. *F* values are results of a two-way ANOVA comparing lengths among cruises and between stations.

	Station		*F*		
Cruise	Inshore	Offshore	Cruise	Station	Cruise × Station
Feb. 1980	15.2 (0.3)	8.9 (0.2)	21.8**	81.8**	62.6**
Dec. 1980	13.5 (0.3)	8.7 (0.3)			
Feb. 1981	12.3 (0.2)	12.3 (0.2)			

**$P < 0.001$.

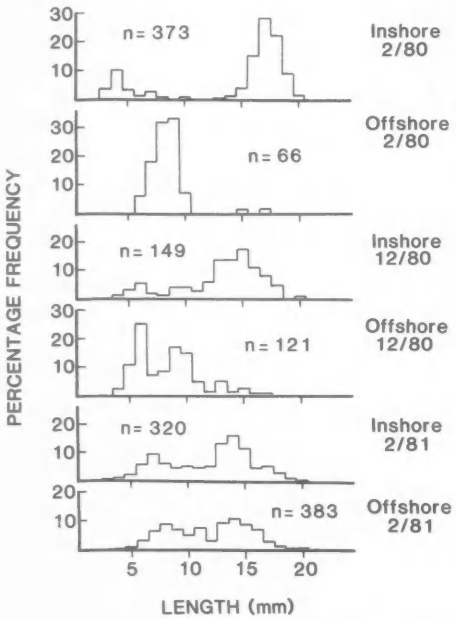

FIGURE 2.—Length-frequency distributions of gulf menhaden larvae collected from inshore (18 m isobath) and offshore (91 and 183 m isobaths combined) stations off Southwest Pass, Louisiana, on three cruises (February 1980, December 1980, and February 1981). n = number of larvae measured.

TABLE 3.—Mean density (larvae × 100 m^{-3}) at each discrete depth during each time period. MOCNESS casts in which no larvae of the target species were caught at any of the discrete depths were not included in calculation of means.

	Time			
Station/species	0600	1200	1800	2400
Inshore				
Total larvae				
1 m	68.23	120.97	341.10	76.36
6 m	56.01	25.76	144.20	86.82
12 m	42.44	25.24	69.20	173.78
Gulf menhaden				
1 m	31.72	37.35	48.83	12.44
6 m	4.54	0.14	101.06	22.74
12 m	13.16	0.60	29.93	22.37
Spot				
1 m	1.36	1.99	154.35	8.13
6 m	0.76	1.04	2.02	5.12
12 m	0.82	0.39	1.79	34.63
Atlantic croaker				
1 m	2.05	1.07	2.47	1.62
6 m	4.08	4.05	3.61	1.66
12 m	12.65	1.32	4.57	6.43
Offshore				
Total larvae				
1 m	103.90	57.37	57.64	49.65
30 m	35.41	21.30	63.37	42.37
70 m	23.38	8.35	14.93	14.29
Gulf menhaden				
1 m	23.70	35.60	14.36	14.19
30 m	7.47	0.00	7.77	3.76
70 m	0.22	0.39	0.42	0.29

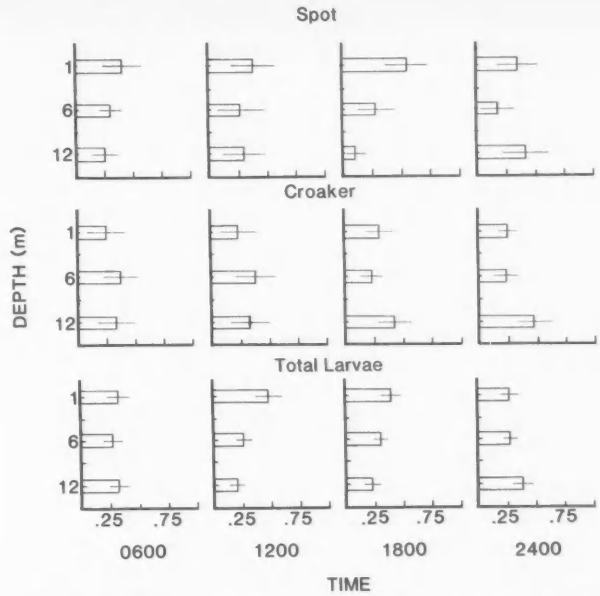

FIGURE 3.—Mean percentage of Atlantic croaker, spot, and total larvae collected at three discrete depths at inshore stations (18 m isobath). Error bars are standard errors.

mean densities were greater in surface waters at 1200 and 1800 h and in deeper waters at 2400 h (Table 3). The high mean densities of spot in surface waters at 1800 h and at 12 m at 2400 h (Table 3) were related to the encounter with the previously mentioned patch of larvae at Cape San Blas. When mean relative proportions were considered, however, these trends were moderated (Fig. 3). Although mean densities suggested a propensity for Atlantic croaker larvae to occur in deeper waters (Table 3), this trend also weakened when relative proportions were considered (Fig. 3). Gulf menhaden larvae in all three length groups were highly concentrated at the surface at 1200 h, but showed inconsistent patterns at other times (Fig. 4).

At the offshore stations (91 and 183 m), where there was a broader scale for vertical distribution, total larvae were generally less abundant at the deepest sampling depth (70 m, Table 3), but mean relative distributions indicated only slight trends (Fig. 5). Gulf menhaden larvae at offshore stations had greater densities at the surface at all times, with few larvae present at 70 m (Table 3). They again occurred almost exclusively in surface samples at 1200 h (Fig. 5). (Spot and Atlantic croaker were too rare at the offshore stations to allow examination of vertical distribution.)

Comparison of MOCNESS casts in thermally stratified versus isothermal water columns indicated that the presence of a weak thermocline did not inhibit vertical movement by any of the three target species or total fish larvae. Depth distributions were similar regardless of the thermal structure of the water. In most cases where a thermocline occurred, it was reversed, with colder water overlying warmer water, and a temperature difference of $<5^{\circ}C$, the result of the Mississippi River plume.

DISCUSSION

High densities of gulf menhaden larvae at the Southwest Pass stations support the conclusions of Fore (1970) and Christmas and Waller (1975[5]) that spawning is concentrated around the Missis-

[5]Christmas, J. Y., and R. S. Waller. 1975. Location and time of menhaden spawning in the Gulf of Mexico. Unpubl. manuscr. Gulf Coast Laboratory, Ocean Springs, MS 39564.

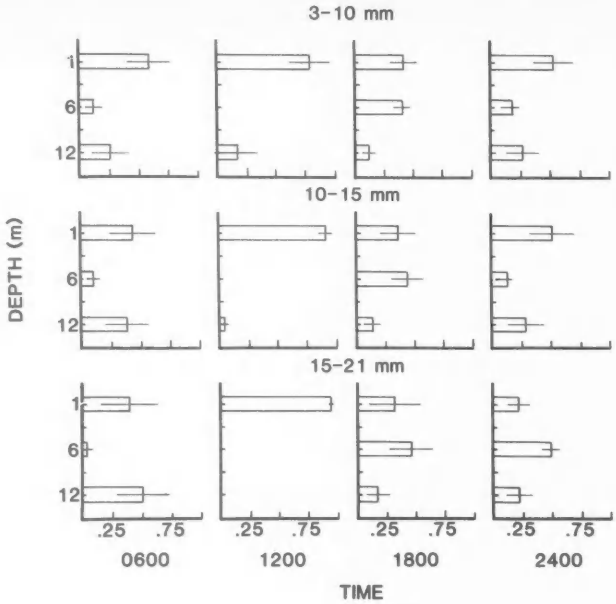

FIGURE 4.—Mean percentage of gulf menhaden larvae, divided into three size groups, collected at three discrete depths at inshore stations (18 m isobath). Error bars are standard errors.

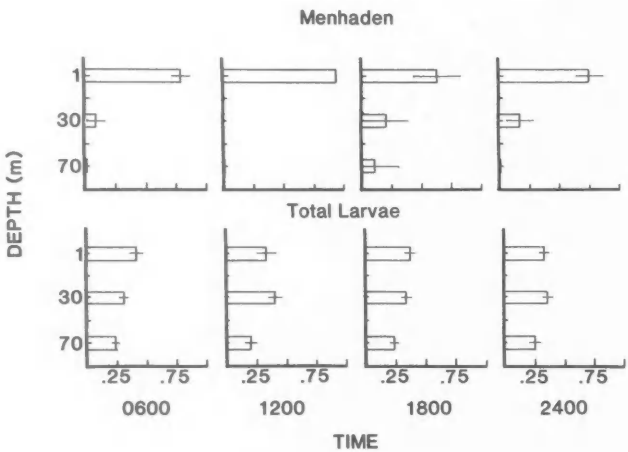

FIGURE 5.—Mean percentage of gulf menhaden and total larvae collected at three discrete depths at offshore stations (91 and 183 m isobaths). Error bars are standard errors.

sippi River Delta. In addition, Atlantic croaker larvae were rarely caught except at the inshore Southwest Pass station. High levels of nutrients (Riley 1937) and the resultant high plankton biomass in this region (Bogdanov et al. 1968) may make conditions exceptionally favorable for fish larvae.

Densities of all three target species showed a clear decline from inshore to offshore waters (Table 1). Shaw et al. (1985b) found a similar pattern for gulf menhaden larvae farther west along the Louisiana coast; densities were greatest in waters between the 14 and 24 m isobaths, with a shift in concentration to very nearshore waters by the end of the spawning season. The major spawning efforts of gulf menhaden, spot, and Atlantic croaker appear to occur in a relatively narrow band along the coast.

Size-frequency distributions of gulf menhaden larvae along the Southwest Pass transect showed that offshore stations were populated with smaller larvae on two of three cruises (Fig. 2, Table 2), but off western Louisiana, Shaw et al. (1985a) detected no difference in the size distribution of gulf menhaden from the 183 m isobath to inshore waters, except at stations immediately adjacent to shore (approximately 9 m in depth). Our observed pattern of decreasing size with distance from shore could arise either by adults spawning offshore and larvae growing as they move toward estuarine nursery grounds, or from serial spawning as adults move offshore during the protracted spawning season. The latter pattern is corroborated by Roithmayr and Waller (1963) and Fore (1970).

Only gulf menhaden showed clear evidence of a diel pattern in vertical distribution; they were concentrated almost exclusively at the surface at midday, but were more vertically dispersed at night at inshore stations. Size did not determine which larvae descended by dusk, because the vertical distribution was similar across all three size groups. In contrast, vertical migration of yellowtail flounder, *Limanda ferruginea*, and Atlantic herring, *Clupea harengus*, larvae varies with size, with smaller individuals remaining closer to the water surface (Smith et al. 1978; Wood 1971). Depth distributions of northern anchovy, *Engraulis mordax*, and white croaker, *Genyonemus lineatus*, also vary with age, with older larvae concentrating in deeper waters (Brewer and Kleppel 1986).

Gulf menhaden larvae >12 mm SL have deflated swimbladders by day and inflated swimbladders at night, achieved by swallowing air at the surface (Hoss and Phonlor 1984). This behavior, common among clupeoids (Hunter and Sanchez 1976; Uotani 1973), is thought to allow passive depth maintenance during nonfeeding hours at night (Hunter and Sanchez 1976). The observed depth distribution of gulf menhaden indicates that larvae must actively swim to stay at the surface during daylight hours. Apparently, the larvae slowly sink at night despite having gas in their swimbladders, and are, therefore, distributed at various depths. Data from offshore stations (Fig. 4) suggests, however, that most larvae are able to maintain their position within the upper 30 m of the water column.

The pattern of vertical distribution of gulf menhaden is opposite of that reported for numerous other species, in which larvae rise toward the surface at night and descend by day (e.g., Seliverstov 1974; Smith et al. 1978; Kendall and Naplin 1981; Sameoto 1982, 1984). A reversed pattern has also been observed for *Gadus macrocephalus* (Boehlert et al. 1985) and *Ammodytes personatus* (Yamashita et al. 1985). Yamashita et al. (1985) suggested that diurnal feeding requirements and nocturnal avoidance of upwardly migrating predators influence the vertical migration of *Ammodytes*. The behavior of Atlantic menhaden, *Brevoortia tyrannus*, is probably similar to gulf menhaden, as they are also reported to be more concentrated in surface waters by day than night (Thayer et al. 1983).

The presence of a weak thermocline with a gradient of <5°C did not appear to influence the vertical movement of fish larvae in this study. Other studies have reached conflicting conclusions. Ahlstrom (1959) and Loeb (1980) found thermal stratification with a temperature difference of 8° to 10°C very important in determining vertical distribution. Smith et al. (1978), Kendall and Naplin (1981), and Sameoto (1982), however, found that thermal gradients of 8° to 14°C did not inhibit vertical migration. The depth of the water column, the intensity of temperature change at the thermocline, and behavior of the species in question likely influence migration patterns. In relatively shallow water (Smith et al. 1978; Kendall and Naplin 1981; this study), thermal stratification appears less of a barrier than in deeper water. In this study larvae of gulf menhaden, spot, and Atlantic croaker largely remained within the upper 30 m, even when the water column was well-mixed to a depth of over 100 m. As we found for gulf menhaden, Brewer

and Kleppel (1986) noted significant diurnal depth stratification of larvae in the absence of thermal stratification. Absolute depths may be more important than thermal layers in determining vertical distribution when temperature differences are small.

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DISTRIBUTION OF WITCH FLOUNDER, *GLYPTOCEPHALUS CYNOGLOSSUS*, IN THE SOUTHERN LABRADOR AND EASTERN NEWFOUNDLAND AREA AND CHANGES IN CERTAIN BIOLOGICAL PARAMETERS AFTER 20 YEARS OF EXPLOITATION

W. R. BOWERING[1]

ABSTRACT

Witch flounder were distributed throughout the study area from Hamilton Inlet Bank to the Northern Grand Bank. The main concentrations were located in Hawke Channel, the channel around Funk Island Bank, and the north slopes of the Grand Bank. While these are believed to be the main locations of three separate stocks, there was no apparent discontinuity in the distribution among the three NAFO Divisions investigated. It is clear, however, that the stock located in NAFO Div. 3K is considerably larger than the combined stocks of NAFO Div. 2J and 3L. Stocks showed minimal variations in depth and temperature preference. Depth and temperature preferences were demonstrated for different size and age-classes of fish. There were substantial reductions in the number of age groups composing the stocks; this was complemented by increases in mean sizes at age for each stock although the magnitude of this increase varied from one stock to another. There was evidence of reduced size and age at sexual maturity in some instances, however, in most cases the results are difficult to explain. These changes in population dynamics are discussed in relation to changes in exploitation over the past 20 years.

Prior to the early 1960's, fishing for witch flounder, *Glyptocephalus cynoglossus*, in the area of southern Labrador and eastern Newfoundland was practically nonexistent. When a significant fishery began in the early 1960's, catches were taken from the accumulated virgin stock in NAFO (Northwest Atlantic Fisheries Organization) Div. 2J, 3K, and 3L (Fig. 1) primarily by large offshore otter trawlers from Canada, Poland, and the Soviet Union. Significant catches were also taken by Newfoundland gill net fishermen in the deepwater bays of northeastern Newfoundland (Bowering and Pitt 1974) (Fig. 1).

Annual landings increased dramatically from <1,000 t in 1963 to peak at nearly 24,000 t in 1973 (Fig. 2). It should be noted, however, that catch statistics prior to 1973 were based upon a formula for breaking down catches of unspecified flounder catches into species and may not be totally accurate. Subsequent to 1973, landings declined nearly as dramatically as they had risen until they stabilized at about 3,000-5,000 t annually over the period 1980-85. In 1973, ICNAF (International Commission for the Northwest Atlantic Fisheries) decided to place catch quota regulations on witch flounder in this area; for management purposes witch flounder in Div. 2J, 3K, and 3L was treated as a single unit (Fig. 1). The first TAC (total allowable catch) was placed on this stock in 1974 at a level of 22,000 t, which was subsequently reduced to 17,000 t for 1975-80, based upon an assessment by Bowering and Pitt (1974). An updated assessment by Bowering and Baird (1980) advised a TAC of 8,000 t for 1981, and this TAC level was in effect up to 1986. The TAC for 1987 was further reduced to 4,000 t.

Although, for management purposes, witch flounder in Div. 2J, 3K, and 3L is considered a single population (stock), stock delineation studies have shown this not to be the case. Fairbairn (1981), using biochemical systematics (electrophoresis), distinguished two separate breeding stocks in this area, one in Div. 3K and one in Div. 3L. No data were available from Div. 2J. Bowering and Misra (1982), employing a new multivariate analysis technique on meristic data, corroborated Fairbairn's (1981) findings and also identified a separate stock in Div. 2J.

The purpose of this paper is to describe the distribution of witch flounder throughout this management zone during recent years and to examine age, growth, and sexual maturity patterns by di-

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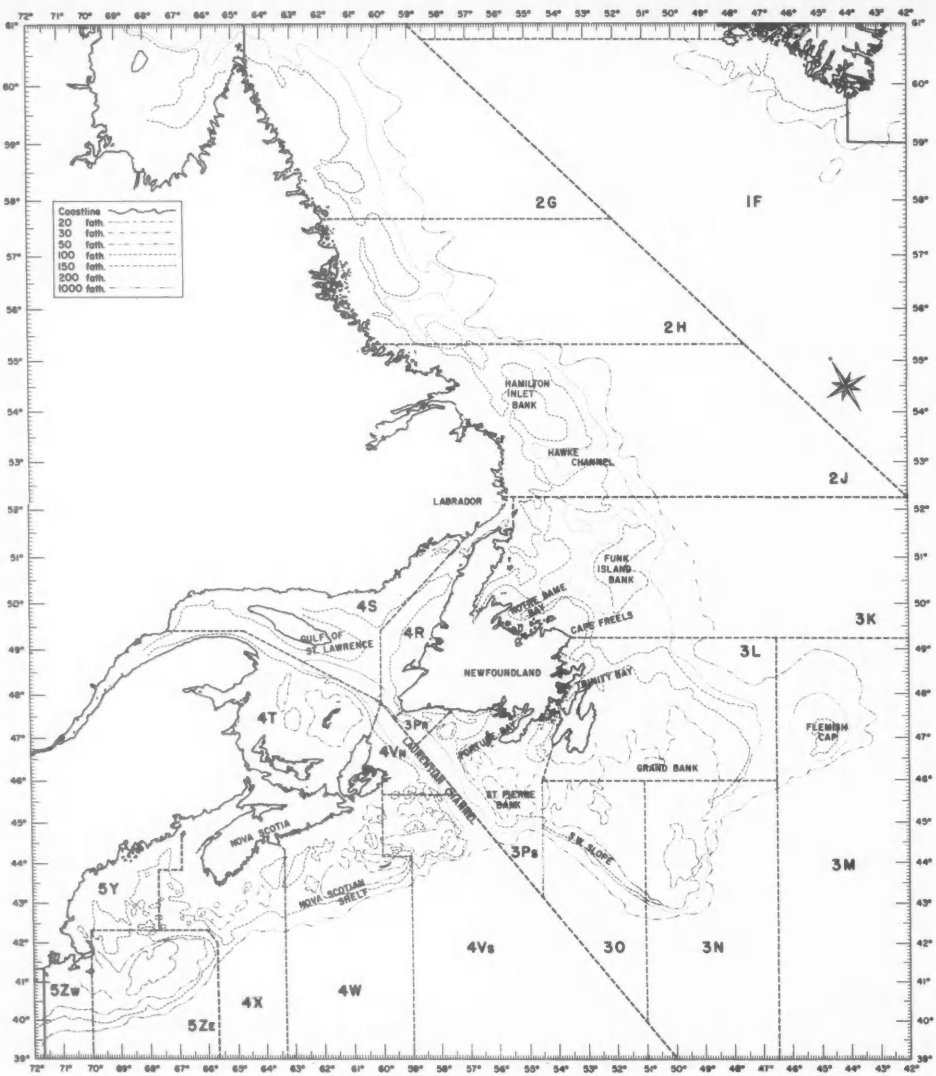

FIGURE 1.—Map of major place names mentioned in the text.

vision (since they contain different stocks) during, and subsequent to, years of heaviest exploitation.

MATERIALS AND METHODS

All data were collected during research vessel surveys for groundfish, carried out on an annual basis by Newfoundland-based research vessels or chartered vessels used for research purposes. All vessels used otter trawls with small mesh (12.7-28.1 mm) nylon liners in the cod end to prevent the escape of juvenile fish. Catch records of sets which experienced enough damage to the gear

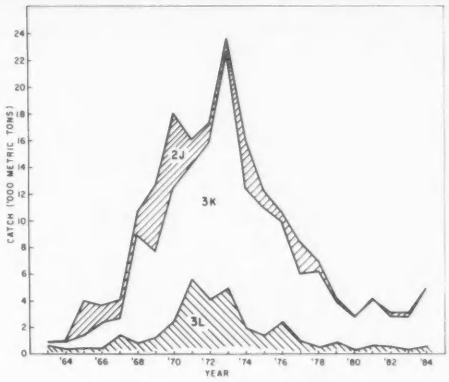

FIGURE 2.—Nominal catches of witch flounder in NAFO Div. 2J, 3K, and 3L from 1963 to 1984.

that overall catch might be affected were not included in the analyses. All fishing tows were of 30-min duration. At the end of each set, bottom temperature was measured using an expendable bathythermograph (XBT).

The geographic distribution and relative abundance is shown by indicating, in 1/2° latitude and 1° longitude rectangles, the average numbers of fish caught per 30-min set. A preliminary examination of distribution of witch flounder by year (all divisions) and season (Div. 3L only where enough seasonal data were available) showed no differences in geographic distribution; therefore, all trips were combined for the period 1977-83. These years were chosen for the distribution study since surveys during this period were based upon random distribution of sets throughout the fishing area whereas prior to this time some areas were surveyed using fixed station line transects not covering the whole area. The number of sets used in the presentation of the distribution is shown in Figure 3.

Ages were determined from otoliths (Powles and Kennedy 1967). Age composition is presented for males and females separately by division. Comparisons of age composition were made for Div. 2J for the periods 1973-78 and 1979-83, Div. 3K for the periods 1970-78 and 1979-83, and Div. 3L for the periods 1968-78 and 1979-83. For Div. 2J and 3K most data were collected during the last quarter, whereas for Div. 3L most data were collected over the last half of the year. However, considering the extent of the data and the very slow growth rate of witch flounder (Bowering 1976), slight differences in the timing of data collection are not sufficient to invalidate comparisons among divisions.

Growth (cm) was expressed in terms of log-log regressions (Log_e Length $= a + b$ $\log_e$ Age (years)). Growth curves were computed for each of the age compositions stated above using data for each fish and not mean length at age. Differences in weight at age were then calculated between the earlier period and later period for each division by applying the length-weight relationship of Bowering and Stansbury (1984) to the observed mean length at age.

The maturity rates were calculated as the length (cm) and age (years) at which 50% of fish were mature (M_{50}) as determined by probit analysis according to the method of Bliss (1952) as applied to witch flounder in the Gulf of St. Lawrence by Bowering and Brodie (1984). The results are presented with 95% fiducial limits. Males for Div. 2J were not included in the calculations due to too low numbers of immature fish in the samples to allow for a significant probit analysis.

RESULTS

Geographic Distribution and Relative Abundance

Witch flounder was caught throughout the stock management zone of Div. 2J, 3K, and 3L from the northern tip of Hamilton Bank to the northern half of the Newfoundland Grand Bank (Fig. 4). Catches were insignificant in the Hamilton Bank area of Div. 2J with mean numbers per 30-min set generally <1.0. The general area of highest abundance in this division was to the south in the Hawke Channel. Here mean numbers per set ranged from about 2.0 in rectangle Q16 to 11.0 in P17, the highest in Div. 2J (Fig. 4). In Div. 3K, mean numbers per set per rectangle were considerably higher than those in Div. 2J. For many rectangles the mean numbers per set were in excess of 10.0. The general areas of highest abundance occurred along the deep waters around Funk Island Bank where mean catches ranged from about 13 to 53 fish/set. The highest density occurred in rectangles P21, P22, Q22, Q23, and R24 where mean catches ranged from 43 to 53 fish/set. In Div. 3L the only significant catches occurred along the northern slope and northeast cape of the Newfoundland Grand Bank. In this area, catches ranged from about 2 to

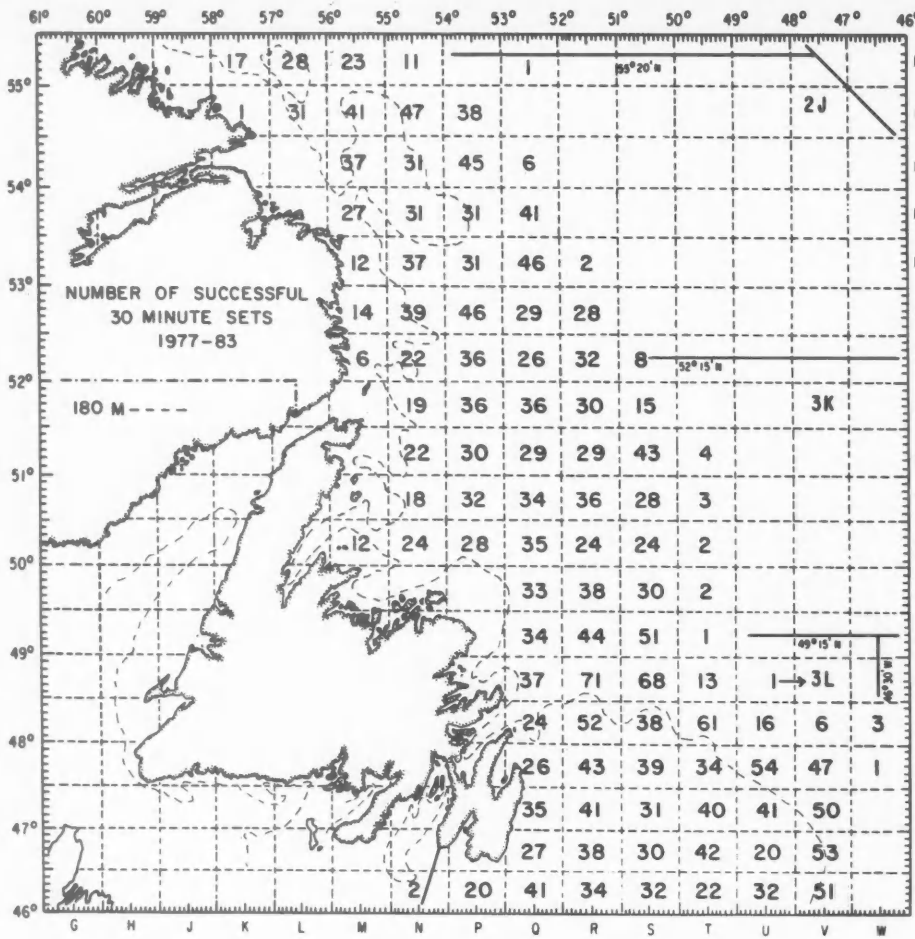

FIGURE 3.—Number of successful 30-min bottom trawl sets per (rectangle) in NAFO Div. 2J, 3K, and 3L by Canadian research vessels from 1977 to 1983.

15 fish. The highest mean catch was 23 and occurred in rectangle W27. This was based upon only 1 set however (Fig. 3). On the other hand, the second highest mean catch per set was 15 fish in the adjacent rectangle V27, based upon 47 sets (Figs. 3, 4). It should be noted also that some of the highest mean numbers per set occurred due east of Cape Freels along the dividing line between Div. 3K and 3L. Catches in the southern portion of Div. 3L were insignificant with most rectangles having mean catches of about 0.1 fish/set.

Distribution by Depth and Temperature

Distribution by 100 m depth intervals of witch flounder is presented in Figure 5. For Div. 2J, witch flounder were caught in depths ranging from 101 to 900 m. However, only the depth range

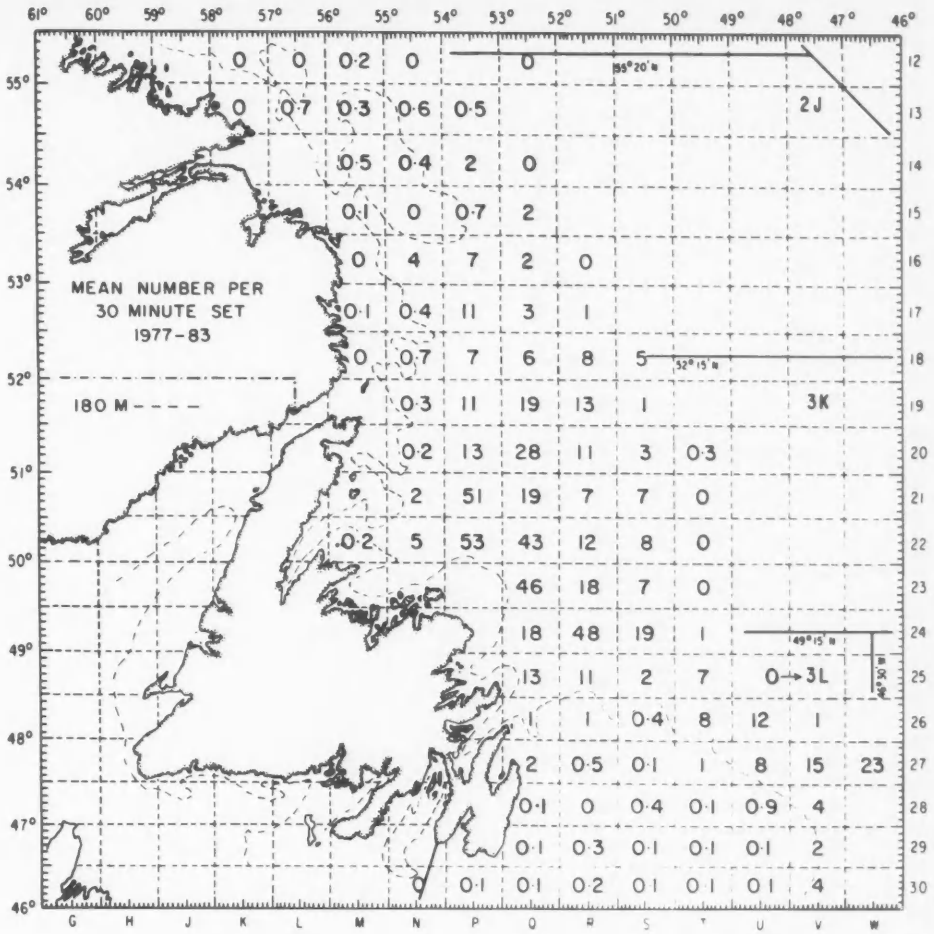

FIGURE 4.—Mean number of witch flounder caught per 30-min set per (rectangle) in NAFO Div. 2J, 3K, and 3L during 1977-83 by Canadian research vessels.

of 301-600 m showed any significant numbers with a peak at 501-600 m after which numbers declined rapidly to near zero. In Div. 3K witch flounder were caught in depths ranging from 201 to 900 m. Only one set was conducted in depths <201 m which yielded no catch (Fig. 5). The mean catch per set increased very sharply from this depth to peak at 401-500 m. The mean catch per set of about 47 fish at that depth interval was significantly different than mean catches in all other depths (Fig. 5). Mean catches beyond 500 m dropped off dramatically to near zero beyond 600 m. In Div. 3L witch flounder were caught in depths ranging from <101 to 800 m. No sets were conducted beyond 800 m (Fig. 5). Mean catches in depths <201 m were close to zero, based upon 864 sets. The increase in mean catch per set was similar to that of Div. 3K and peaked at 301-500 m, however, there was considerable overlap in confidence limits (Fig. 5). Unlike Div. 2J and 3K there

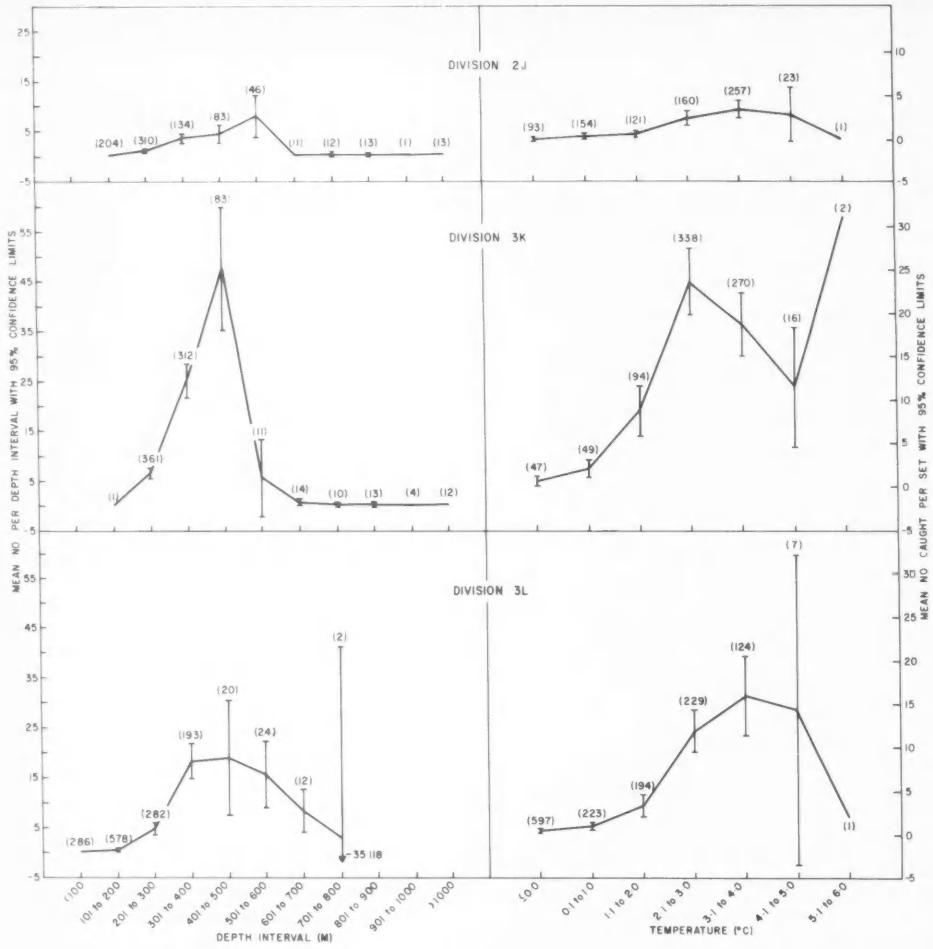

FIGURE 5.—Mean numbers of witch flounder caught per 30-min set per depth and temperature interval in NAFO Div. 2J, 3K, and 3L from 1977 to 1983 with 95% confidence limits. (Numbers in parentheses are number of sets observed.)

was not a marked decline in mean catch beyond the peak with substantial numbers of witch flounder being caught in depths up to 700 m.

Distribution of witch flounder by bottom temperature is also presented in Figure 5. Because of the very low catches in Div. 2J, it is difficult to identify discrete optimum temperatures. There was a slight increasing trend, however, from 1.1°-2.0°C to peak at 3.1°-4.0°C and decline beyond that. In Div. 3K witch flounder were caught in bottom temperatures from ≤0.0° to 6.0°C. There was a marked increasing trend from the 0.1°-1.0°C interval to peak at a temperature range of 2.1°-3.0°C beyond which the mean catch per set declined. The highest mean catch per set occurred at 5.1°-6.0°C. However, this resulted from one large catch in one of the two sets at this interval giving extremely wide 95% confidence limits. In Div. 3L an increasing trend was evidenced similar to that shown for Div. 3K, however, it was

slightly less marked and peaked at 3.1°-4.0°C and then declined. The data were too few at the higher temperatures to evaluate the significance of the decline.

Since depth and bottom temperature are generally related, a mean catch per 30-min set by depth and temperature is presented in Figure 6. When depth and bottom temperature are combined the range of best catches for Div. 2J is about 201-600 m and 2.1°-5.0°C. For Div. 3K it is about 201-500 m and 2.1°-4.0°C. For Div. 3L the range of best catches appears to be about 301-600 m and 2.1°-4.0°C. Despite the variations in depth and temperature distribution throughout the three divisions shown in Figures 5 and 6, the depth and temperature relationships among the divisions did not differ greatly or at least not among the locations fished (Fig. 7).

Mean length (cm) and mean age (years) for each depth and temperature interval are presented in Figures 8 and 9 respectively. Mean lengths and ages by depth interval for the three divisions showed similar trends in that they were highest in the shallower depths and declined to reach a low at some intermediate depth then increased and stabilized. For the three divisions combined there was a significant decrease in mean length from about 52 cm at ≤100 m to about 43 cm at 401-500 m. Mean lengths increased beyond this to near 47 cm and stabilized in the 600-900 m range. The mean age decreased from near 11 years old at ≤100 m to about 8 years old at 401-500 m. It stabilized at about 10 years old beyond that.

For all three divisions there was a general declining trend in mean length and age from the lower to intermediate temperatures (Fig. 9). In all cases (except Div. 2J where catches were generally low), the lowest mean size and age occurred at the 3.1°-4.0°C range. For the three divisions combined, there was a significant decline in mean length from about 50.5 cm and 10.0 years old in the 0.1°-1.0°C temperature range to about 45.5 cm and 9 years old in the 3.1°-4.0° temperature range. Beyond this range the mean length and age increased again.

Age Composition

The age compositions of male and female witch flounder by division and time period are presented in Figure 10. For Div. 2J during 1973-78,

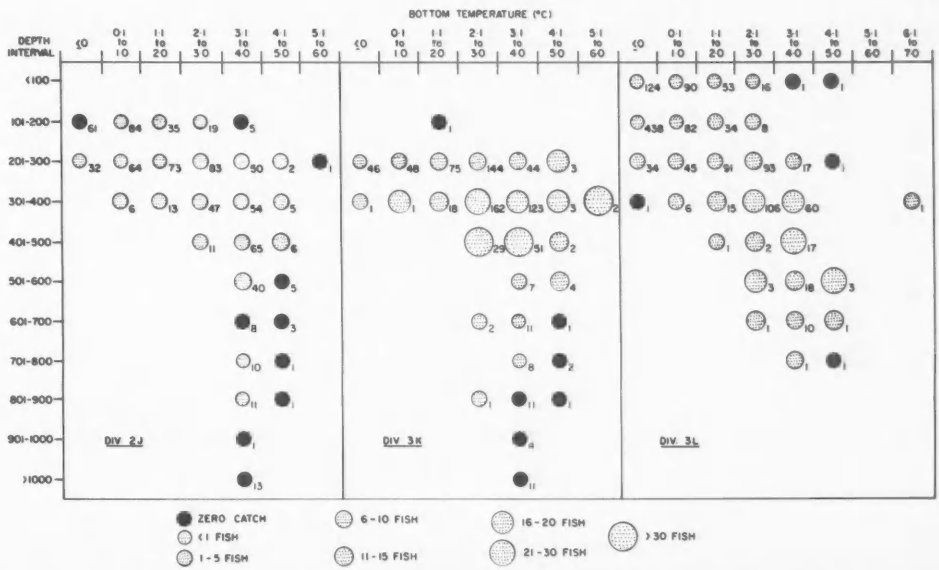

FIGURE 6.—Mean number of witch flounder caught per 30-min set by depth and temperature intervals in NAFO Div. 2J, 3K, and 3L from 1977 to 1983. (Numbers in parentheses are number of sets observed.)

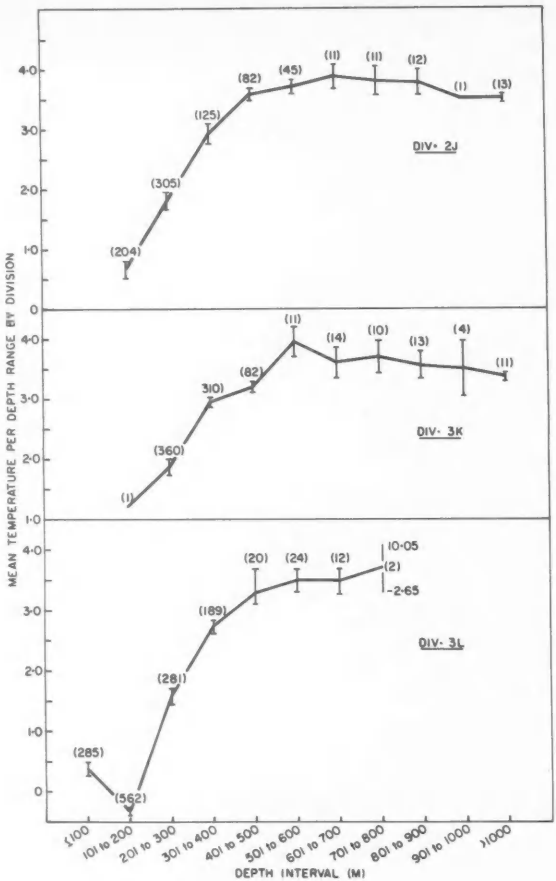

FIGURE 7.—Mean temperature with 95% confidence limits per depth interval in NAFO Div. 2J, 3K, and 3L from 1977 to 1983 as determined from research vessel surveys. The number of sets used in the calculations are shown in brackets for each depth interval.

males and females in the catches ranged from 6 to 18 years old and 4 to 21 years respectively. More than 50% of the males were older than age 10 and more than 50% of the females were older than age 12. In Div. 2J during 1979-83 the males and females ranged from 4 to 11 years old and 6 to 13 years old respectively. Less than 2% of the males were older than age 10 and less than 2% of the females were older than age 12.

For Div. 3K during 1970-78, males and females in the catches ranged from 3 to 16 years old and 3 to 22 years old respectively. About 50% of the males were older than 8 years while more than 50% of the females were older than 10 years. In Div. 3K during 1979-83 the males and females ranged from 2 to 13 years old and 2 to 14 years old respectively. About 30% of the males were older than 8 years with about 30% of the females older than 10 years.

In Div. 3L during 1968-78, males and females in the catches ranged from 2 to 18 years old and 4 to 23 years old respectively. About 50% of the males were older than 11 years and about 50% of the females were older than 12 years. During

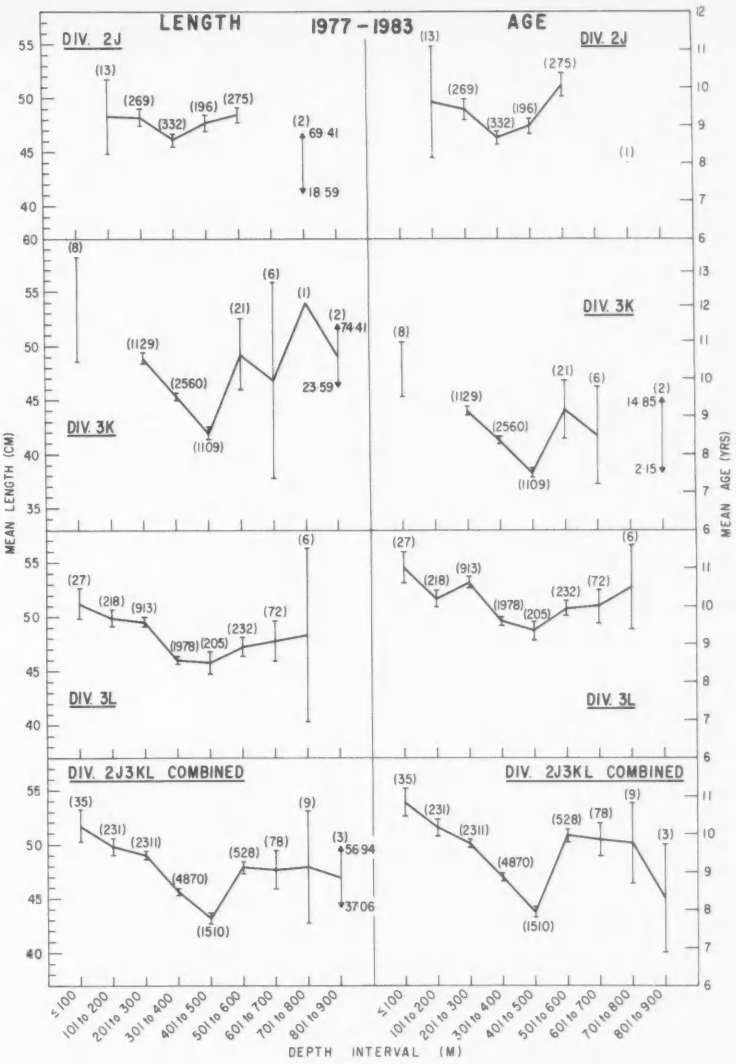

FIGURE 8.—Mean length (cm) and mean age (years) of witch flounder per depth interval in Div. 2J, 3K, and 3L separately and combined from research vessel surveys during 1977-83. (Number in brackets refers to the number of fish observed.)

1979-83 in Div. 3L, males and females ranged from 3 to 13 years old and 3 to 17 years old respectively. Only about 5% of the males were older than 11 years and about 8% of the females were older than 12 years.

Growth Curves

Growth curves of male and female witch flounder with mean lengths at age are presented in Figure 11 and Table 1. Clearly, males do not grow as fast as females over the life span. Growth rates

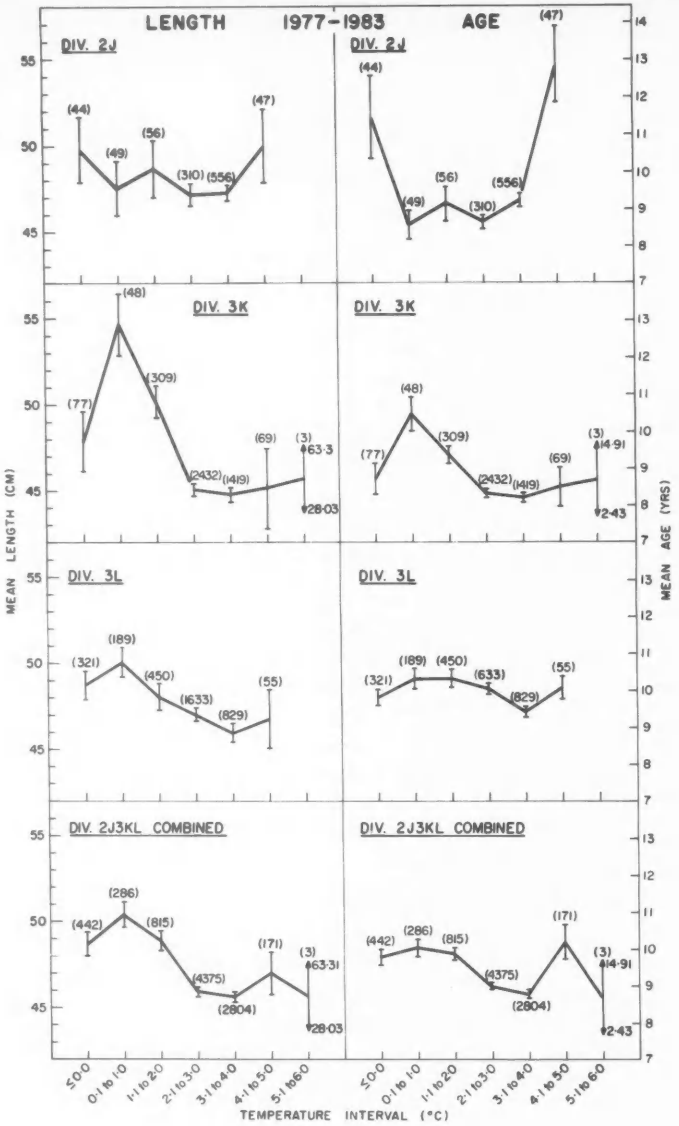

FIGURE 9.—Mean length (cm) and mean age (years) of witch flounder per temperature interval in Div. 2J, 3K, and 3L separately and combined from research vessel surveys during 1977-83. (Number in brackets refers to the number of fish observed.)

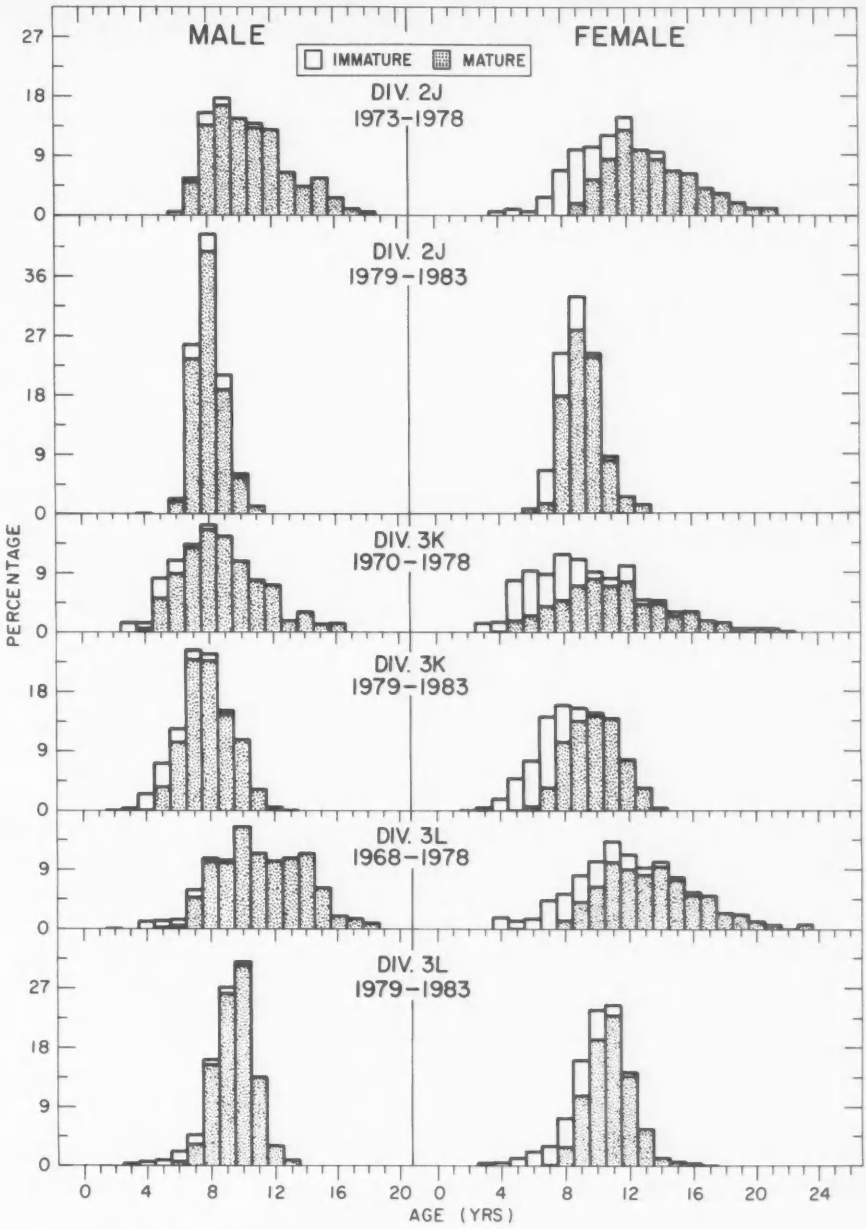

FIGURE 10.—Age compositions of male and female witch flounder in Div. 2J, 3K, and 3L for various time periods between 1968 and 1983. (Shaded areas represent proportions mature at each age.)

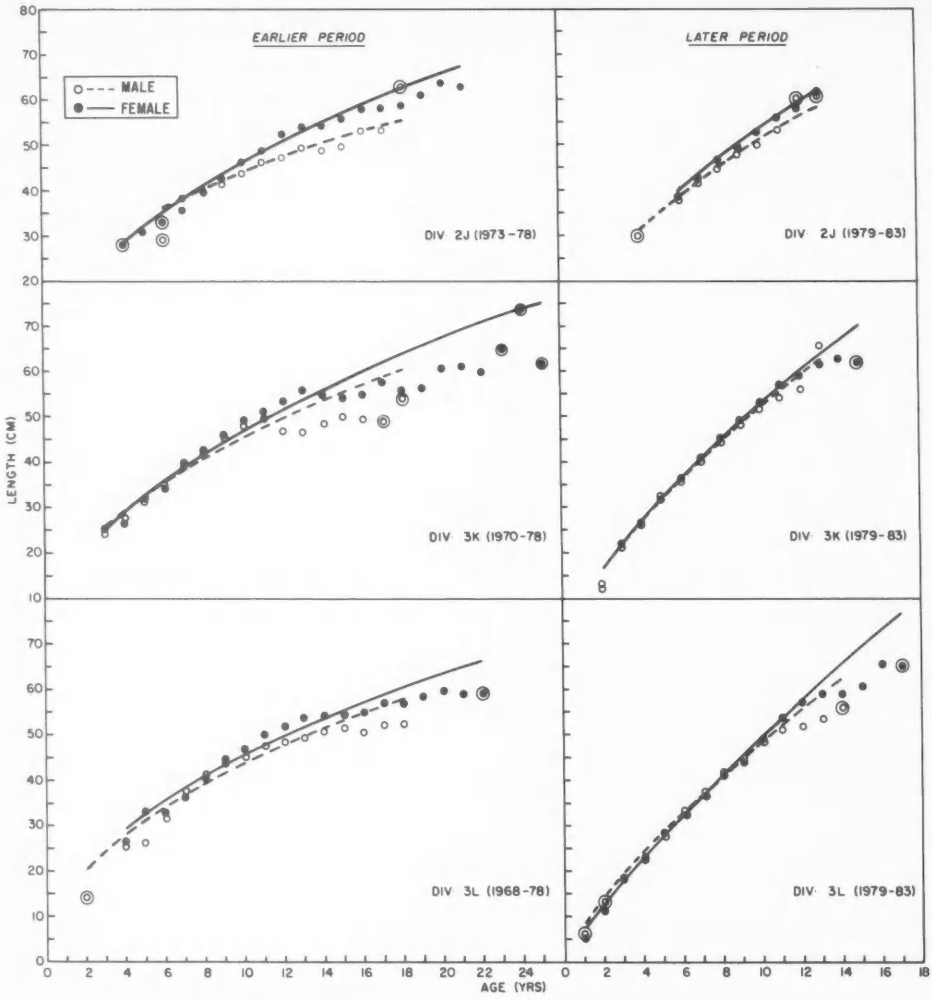

FIGURE 11.—A comparison between two time periods for growth curves of male and female witch flounder in NAFO Div. 2J, 3K, and 3L (circled points indicate only one observation).

(using slopes of the curves as an expression of rate of change of length with age) between the sexes are similar up to about ages 10-12 after which they diverge, particularly if the mean length at age is used as a criterion. While the curves do not appear to fit the mean data points very well in the older ages (and to a much lesser degree the very young ages), the correlation coefficients were all high (Table 1) and all highly significant ($P <$ 0.001). The main reason for this is that the number of observations over age 15 is usually <1%. Taking the 1968-78 males in Div. 3L as an example, even adding a second term to the regression (i.e., c (Log_e Age)^2) increases the amount of explained variation by <3%. In nearly all cases the mean data points in older ages are below the fitted lines (Fig. 11) suggesting that if observations were more numerous in the older ages, the actual

TABLE 1.—Regressions and correlation coefficients for age and growth ($\log_e$ length (cm) = a + b $\log_e$ age (years)) of male and female witch flounder in NAFO Divisions 2J, 3K and 3L.

Years	Division	Sex	Correlation coefficient (r)	Slope	Intercept
1973-78	2J	Male	0.80	0.40	2.86
		Female	0.89	0.52	2.63
1979-83	2J	Male	0.82	0.54	2.68
		Female	0.81	0.58	2.64
1970-78	3K	Male	0.82	0.48	2.71
		Female	0.88	0.52	2.65
1979-83	3K	Male	0.93	0.71	2.31
		Female	0.96	0.72	2.30
1968-78	3L	Male	0.78	0.48	2.67
		Female	0.80	0.48	2.71
1979-83	3L	Male	0.91	0.75	2.15
		Female	0.94	0.83	1.99

sizes at age are likely to be lower than here calculated. As a result, the predicted size at age is probably only meaningful up to about age 12 for males and age 15 for females for the earlier period, and age 10 for males and age 12 for females in the later period (Fig. 11). Predicted size for males in Div. 3L during the earlier period is also somewhat biased below age 6. Despite these concerns there has been a substantial increase in size at age of both males and females in all three divisions between the earlier periods and later periods (Fig. 12). A comparison of growth curves by division, for each sex and time period (Fig. 13), suggests that the size at age of witch flounder in Div. 3K is higher in all cases than that of Div. 3L. It is also higher than that of Div. 2J in the earlier period; however, in the later period the mean size at age of the younger fish in Div. 2J is generally higher.

Changes in mean size at age in terms of weight are presented in Table 2. With the exception of some of the younger age groups, where there was some small reduction in size at age over the time period, there was a substantial increase in weight at age for all commercial size age groups (age 7+). The amount of increase in weight at age varied (Table 2) among divisions but most age groups had increases in weight between 25 and 62%.

Sexual Maturity

The proportions of mature and immature witch flounder are shown in Figure 10. Most males caught were in a mature condition for all divisions and time periods. Few mature males caught were <6 years old and all were mature beyond 10 years old. The proportions of mature and immature fish at particular ages, however, varied among divisions and time periods. For females, few mature fish were caught <8 years old in most divisions and time periods, with the possible exception of Div. 3K during 1970-78. Most were mature beyond age 12. As with the males, the proportions mature and immature at particular ages varied among divisions and time periods (Fig. 10).

Lengths and ages at M_{50} with 95% fiducial limits are presented in Figure 14. For males there was no significant difference in length at M_{50} for either Div. 3K or 3L between the earlier and later periods (no data for Div. 2J). For females there was no significant change in M_{50} for Div. 3K between the 1970-78 and 1979-83 periods but there were statistically significant reductions in M_{50} from about 47.0 cm in 1973-78 to about 44.2 cm in 1979-83 for Div. 2J and from about 44.8 cm in 1968-78 to 41.5 in 1979-83 for Div. 3L (Fig. 14).

For males there was no significant change in age at M_{50} for Div. 3K between 1970-78 and 1979-83. However, the age at M_{50} for males in Div. 3L was significantly reduced from about 6.0 years in 1968-78 to 3.5 years in 1979-83 (no data available for Div. 2J). For females there was no significant change in age at M_{50} for Div. 3K between 1970-78 and 1979-83. There was a statistically significant reduction in age at M_{50} for Div. 2J from about 10.4 years in 1973-78 to 7.5 years in 1979-83. There was a slight overlap in fiducial limits for Div. 3L, however, for practical purposes the age at M_{50} was reduced from 9.8 years in 1968-78 to 7.8 years in 1979-83.

DISCUSSION

Distribution

Witch flounder are distributed throughout the management zone from the northern slopes of Hamilton Bank to the northern slopes of the Newfoundland Grand Bank. Bowering (1976) suggested that witch flounder reaches its northern limits in the Northwest Atlantic at the northern slopes of Hamilton Bank although catch statistics of NAFO occasionally reported commercial catches north of here. Unpublished data from surveys in Div. 2G and 2H by the Northwest Altantic Fisheries Center, St. John's, Newfoundland have never reported catches of witch flounder in these areas and support the contention of Bowering (1976) and question the accuracy of some commercial catch reports. For the area surveyed, the distribution of witch flounder presented here is

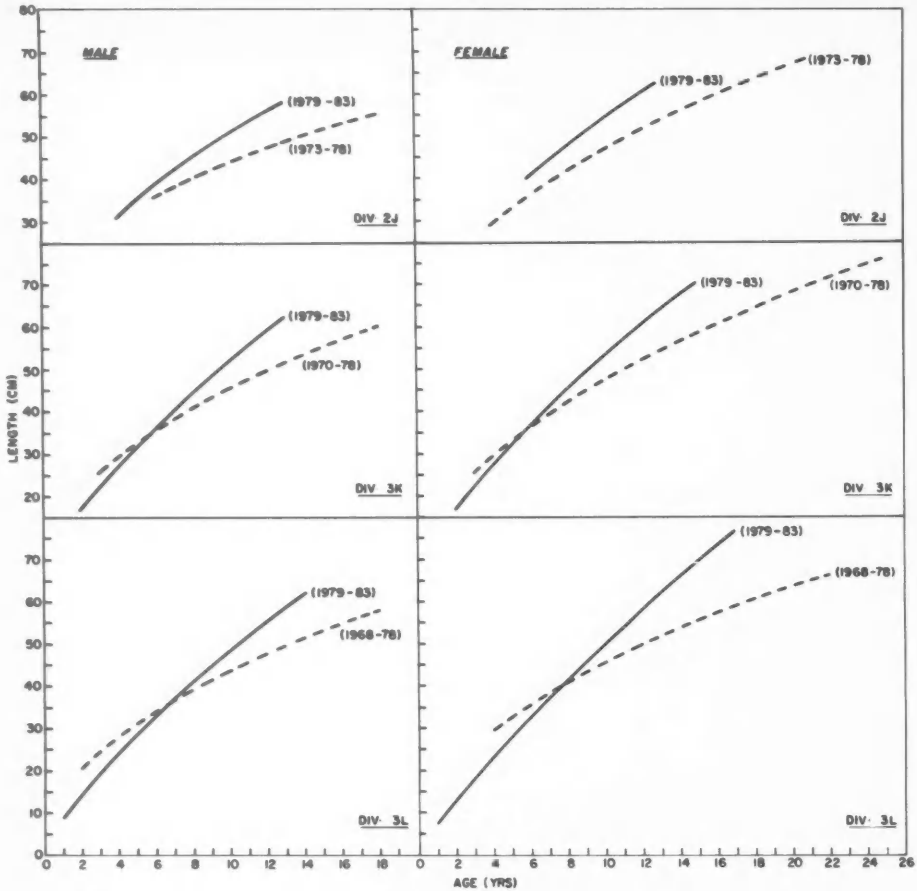

FIGURE 12.—A comparison between male and female witch flounder growth curves in NAFO Div. 2J, 3K, and 3L for earlier and later time periods.

somewhat similar to that published by Bowering (1976) for the 1958-74 period although there was little data available for the southern half of Div. 3K in the Bowering (1976) paper. Although there are no obvious discontinuities in distribution at division boundaries or elsewhere which could account for the occurrence of separate stocks, there are at least three separate stocks of witch flounder reasonably well defined by divisional boundaries as shown by Fairbairn (1981) and Bowering and Misra (1982). This is not to say that some transboundary migrations as adults or through larval drift does not occur when both quite likely do. The largest stock is located in the Div. 3K area according to the catch proportions (Fig. 2) and indices of relative abundance (Fig. 4) presented here. Bowering (1985) reported that minimum trawlable biomass estimates for the management zone during recent years are about 2,500 t, 36,000 t, and 7,800 t for Div. 2J, 3K, and 3L respectively, indicating that the biomass index in Div. 3K is nearly four times higher than Div. 2J and 3L combined.

The major offshore fishing effort towards witch flounder in this zone usually takes place in winter and early spring in areas where prespawning concentrations generally occur, particularly in the

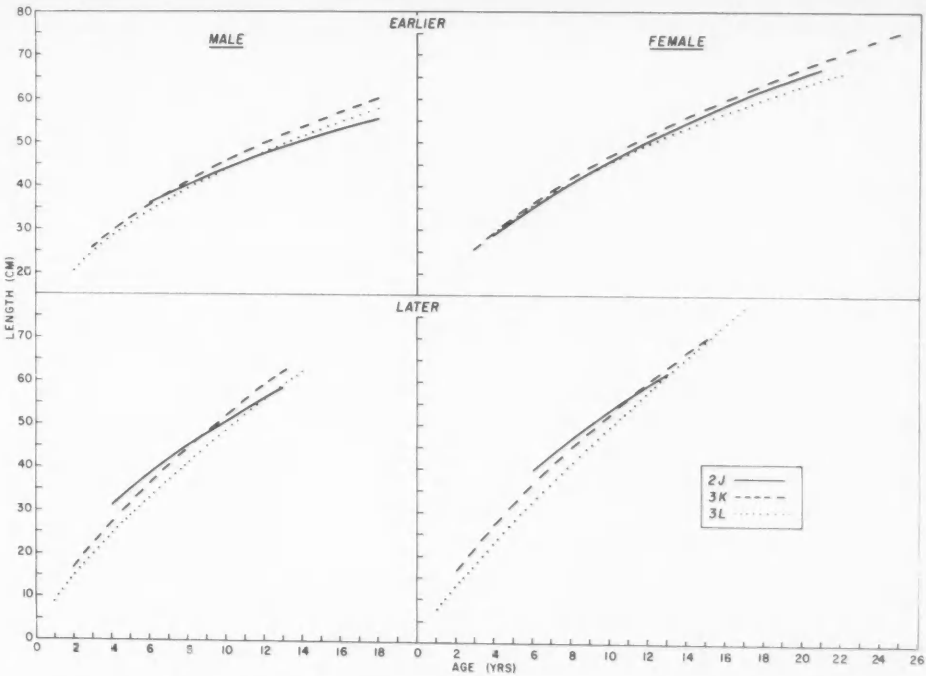

FIGURE 13.—A comparison among divisions for growth curves of male and female witch flounder from earlier and later time periods.

area of Funk Island Deep in Div. 3K (Bowering 1985). In the late 1960's, however, heavy exploitation occurred in the Hawke Channel area of Div. 2J with average annual catches of about 5,000 t as seen in Figure 2. Templeman (1966) reported three research vessel catches of witch flounder in Hawke Channel during April 1963 and 1964 of 2,300 kg, 1,400 kg, and 3,300 kg/hour where these fish appeared to be concentrated. Recent biomass levels of 2,500 t for this area as previously mentioned are now quite low in comparison to the annual catch during the late 1960's even if the catchability coefficient of the survey gear is considerably <1. According to results published in Bowering (1985) the age composition of commercial catches from the management zone in 1976 were as old as 25 years compared to a 15-yr-old maximum in 1984. In 1976, more than 40% of the commercial catch was older than age 12 whereas in 1984 <5% of the catch was older than age 12. It may be that concentrations during prespawning have depleted these stocks, particularly the older, mature fish. This may have contributed to the dramatic decline in landings since the early 1970's. Unfortunately, estimates of biomass for these areas prior to heavy exploitation are not available for comparison.

Witch flounder in this study were not caught deeper than 900 m or at bottom temperatures >7.0°C (higher temperatures were not encountered throughout the study area). Bowering (1976), for the Newfoundland Region as a whole during 1958-74, did not report catches of witch flounder beyond a depth of 869 m, but they were caught at bottom temperatures up to 10°C. Those catches at high temperatures were due mainly to the inclusion of catch data from the southern Grand Bank area (Div. 3N and 3O), where water temperatures are highly influenced by the Gulf Stream. Markle (1975), in studying young witch flounder on the slope off Virginia, caught them down to a depth of 1,408 m and a temperature of 11.3°C. He also found that they were caught in significantly deeper and cooler water in November compared to June. Such a comparison was not possible here. It should be pointed out, however,

TABLE 2.—Changes in mean size at age of witch flounder from 1973-78 to 1979-83 for Division 2J; 1970-78 to 1979-83 for Division 3K; and from 1968-78 to 1979-83 for Division 3L. Only ages common to both periods are included in the comparisons.

	Mean weight (g) Male				Mean weight (g) Female		
Age (yr)	Early	Late	% Difference	Age (yr)	Early	Late	% Difference
			Division 2J				
6	137.53	363.07	164.0	6	215.90	369.73	71.3
7	368.39	486.10	32.0	7	283.25	522.90	84.6
8	430.66	620.16	44.0	8	410.45	723.18	76.2
9	480.01	781.58	62.8	9	528.07	884.41	67.5
10	579.47	907.10	56.5	10	708.68	1,113.32	57.1
11	708.15	1,128.11	59.3	11	860.30	1,355.22	57.5
12	751.14	1,739.31	131.6	12	1,101.59	1,535.95	39.4
13	882.54	1,842.59	108.8	13	1,211.18	1,885.11	55.6
			Division 3K				
3	71.05	44.58	−37.3	3	84.24	47.46	−43.7
4	112.53	99.48	−11.6	4	102.27	99.48	−2.7
5	178.11	199.25	11.9	5	183.34	193.28	5.4
6	257.01	302.54	17.7	6	252.89	300.23	18.7
7	389.19	425.08	9.2	7	402.56	450.79	12.0
8	492.65	602.41	22.3	8	513.94	633.84	23.3
9	654.76	797.71	21.8	9	660.32	842.68	27.6
10	791.92	1,017.10	28.4	10	869.52	1,116.27	28.4
11	872.61	1,202.60	37.8	11	1,003.37	1,416.30	41.2
12	723.18	1,342.57	85.6	12	1,165.69	1,644.10	41.0
13	714.56	2,340.84	227.6	13	1,362.86	1,889.40	38.6
				14	1,277.29	2,062.18	61.5
				15	1,217.44	1,950.18	60.2
			Division 3L				
4	87.79	58.23	−33.7	4	93.95	59.68	−36.5
5	93.95	119.42	27.1	5	215.90	123.66	−42.7
6	179.51	213.39	18.9	6	208.90	209.79	0.4
7	326.43	324.28	−0.7	7	303.71	316.72	4.3
8	451.56	471.19	4.3	8	429.91	466.03	8.4
9	572.11	617.26	7.9	9	626.00	607.17	−3.0
10	632.86	822.34	29.9	10	729.69	845.70	15.9
11	767.38	990.45	29.1	11	920.52	1,168.74	27.0
12	821.16	1,032.36	25.7	12	1,046.37	1,477.51	41.2
13	870.14	1,151.31	32.3	13	1,196.39	1,632.47	36.4
14	962.30	1,367.11	42.1	14	1,211.96	1,628.61	34.4
				15	1,227.67	1,803.88	46.9
				16	1,265.96	2,362.17	86.6
				17	1,445.34	2,299.83	59.1

that Markle (1975) referred only to fish <5 years old, whereas this study has few fish <5 years old.

Witch flounder preferred depths and temperatures at intermediate levels among these samples in Div. 2J, 3K, and 3L. Preferred depth in Div. 3K is more clearly defined than preferred temperature; this is associated with the occurrence of smaller younger fish at intermediate values of the observed ranges. Powles and Kohler (1970) suggested that juveniles in the Gulf of St. Lawrence were in deeper water, separate from the adult, a built-in conservation mechanism for the young. S. J. Walsh (pers. comm.)[2] on the other hand, in examining the distribution of juvenile versus adult witch flounder in the Gulf of St. Lawrence also found that juveniles (<30 cm) had a well-defined preferred depth range whereas the adults (≥30 cm) were distributed over a much wider depth range. For demersal fish it is more common for younger fish to be found in shallower water with most of the larger fish in deeper water (e.g., See Bowering [1984] for Greenland halibut). There is some indication that young American plaice in the Newfoundland-Labrador area may also occupy some intermediate depth over the

[2]S. J. Walsh, Juvenile Flatfish Biologist, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland A1C 5X1, Canada, pers. commun. 1986.

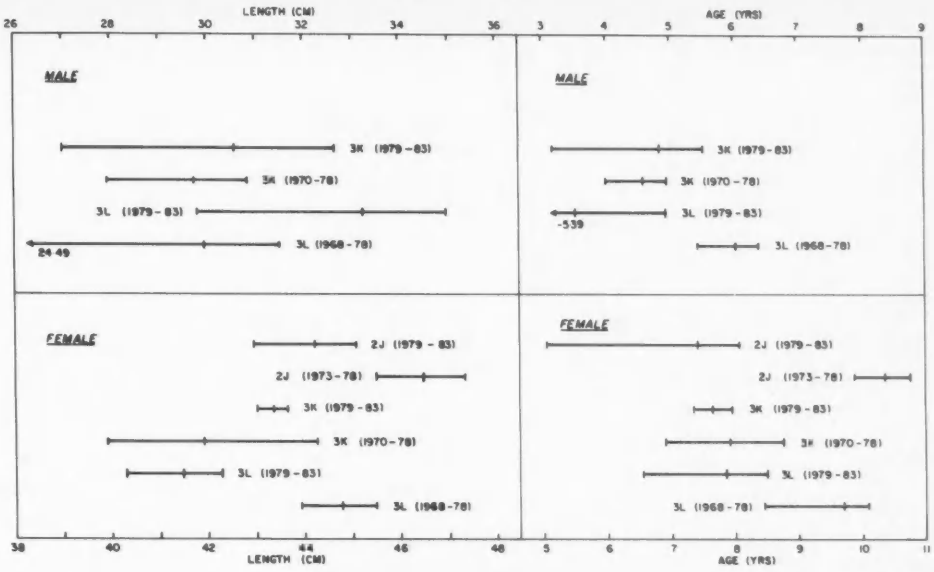

FIGURE 14.—A comparison of lengths (cm) and ages (years) at which 50% of male and female witch flounder are mature from NAFO Div. 2J, 3K, and 3L from earlier and later time periods.

range of its distribution (T. K. Pitt[3]), although the size-depth distribution is not as well defined as presented here for witch flounder. Walsh (1984) concluded, on the other hand, that juvenile plaice occupy the same depth ranges as the adult plaice on the Grand Bank. It should be noted that the results presented in the present paper reflect the depth and temperature preference of young versus old adult witch flounder and not juveniles versus adults as in the studies mentioned.

Age and Growth

The age compositions of witch flounder have changed substantially for all three NAFO Divisions over the study period, with a much shorter life span experienced in recent years. The impact of the reduced life span appears to be greatest on the Div. 2J stock. This may very well be the result of heavy exploitation on prespawning concentrations in the late 1960's when catches were double recent levels of estimated biomass (Bowering 1985). Bowering and Brodie (1984) showed a similar reduction in the life span of witch flounder in the Gulf of St. Lawrence. However, that reduction was more dramatic because it occurred over a shorter time. In 1976, the commercial catches in the Gulf of St. Lawrence comprised fish up to 26 years old compared with a maximum age of 16 years old by 1981. Bowering and Brodie (1984) attributed the sudden change in the population age structure to the fact that almost the entire fishable stock is located in a small area during the winter months when the fishery is most intense. This is particularly true for small stocks such as that in Div. 2J, where it may not be economical to direct effort when the fish are not densely concentrated. In Div. 3K, where the stock biomass is relatively high in comparison to that of Div. 2J and 3L, the fishery is spread more through the year, although the main effort is still directed towards prespawning concentrations. Therefore, the reduction in age groups could be over a longer time period and therefore less dramatic, which seems to be the case here. However, this argument can only be true if, because of such a pattern of fishing, the fishing mortality exerted in areas such as Div. 2J is much higher than for areas such

[3]T. K. Pitt, Section Head, Flatfish Research, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland A1C 5X1, Canada, pers. commun. 1986.

as Div. 3K. Precise information on fishing mortality is unavailable.

The age composition for the 1970-78 period in Div. 3K indicates that little more than 10% of the population was older than 15 years. However, more than 40% of the commercial otter trawl catches in 1976 by both Canada and Poland in Div. 3K were comprised of fish 15 years and older, and more than 30% were 17 years and older (Bowering and Pitt 1977). Thus the impact of the fishery was greatest on the older age groups, and this could explain the rapidity of the disappearance of the population.

Accompanying the reduced age span was an overall increase in size at age for both sexes in all three divisions. The mean size at age for older fish showed a considerable increase from the earlier to later periods examined, whereas the mean size at age for the younger fish was not very different between the two periods. The substantial increase in size of older, commercially exploited fish may be the result of reduced abundance as indicated by the reduced age span. While there is no direct evidence here of density dependent growth, there have been studies published which show that it does occur. Bowering and Brodie (1984) showed that there was a systematic increase in mean size at age of witch flounder in the Gulf of St. Lawrence from 1976 to 1981 for age groups fully recruited to the commercial fishery accompanied by a significant reduction in the age span of the stock. They suggested it was likely the result of increased exploitation and subsequent reduction in abundance. They also showed that because of the increase in growth rate in particular the stock biomass remained relatively stable despite the fact that the stock abundance had been reduced. Unfortunately, estimates of stock abundance and biomass are not available for the earlier periods of this study for comparison.

Bowering (1976) ruled out temperature as a major contributing factor for changes in growth of witch flounder in the Canadian Northwest Atlantic for two reasons: 1) they mainly inhabit depths that are not usually subjected to wide fluctuations in bottom temperature and 2) the growth rates of witch flounder in the more southerly regions are much slower than in the more northerly regions, the opposite of what one would expect if temperature were considered to have a significant influence on its growth rate. Bowering and Brodie (1984) suggested that given the feeding behaviour of adult witch flounder as described by Rae (1969), competition with other species is unlikely to be a significant factor in changes in growth rate, and within species competition is likely to be a more important factor.

Sexual Maturity

It should be pointed out that immature males are not particularly well sampled by the survey gear, and, therefore, the maturity rates may be slightly biased. However, any bias would be consistent for males in all divisions. On the other hand, although younger females are also not well sampled, the first occurrence of mature fish in the samples is reasonably well established. Most of the data here were collected in late summer and early autumn, several months after spawning, and one could have some concern as to the interpretation of immature versus fully recovered gonad condition. I do not feel, however, that witch flounder in these areas studied present significant cause for concern in this regard. The Greenland halibut, a flatfish whose gonad condition is more difficult to interpret, was sampled from northern Labrador in the autumn for visual interpretation of gonad condition complemented by histological analysis by Walsh and Bowering (1981). They found no significant error in the visual (at sea) interpretation of gonad condition, at least for females.

Due to the time of year when sampling occurred, a slight bias in true size and age and maturity may occur; however, it should be consistent throughout the division and time periods examined. Therefore, comparisons should not be biased. Despite such concerns, for the data presented here, it would appear that there was a significant reduction in both mean length and mean age at 50% maturity for both Div. 2J and 3L females and Div. 3L males (for mean age only) over the study period. For Div. 3K there was no significant change in either mean length or mean age at 50% maturity for either males or females over the time period.

Molander (1925) found that for plaice and flounder in the Baltic, maturity appeared at a lower age but at a higher length with increased growth rate, and suggested that when growth rate was poor, the age at maturity was higher. Pitt (1975) found that for American plaice on the Newfoundland Grand Bank, the faster growing fish matured at an earlier age but at approximately the same size. Bowering and Brodie (1984) found similar results for witch flounder in the Gulf of St. Lawrence. It has been suggested,

therefore, that sexual maturity may be more dependent upon body size than on age; the hormones that stimulate sexual maturity may only be produced when the fish and gonads reach a certain size or stage of development. Such a conclusion would not be reached from the results presented here for Div. 2J and 3L, and there are other exceptions in the literature such as those of Fleming (1960) and Pinhorn (1966) for cod in the Newfoundland and Labrador area. It should be noted, however, that although there are statistically significant reductions in mean sizes at maturity presented here, they may not be biologically significant; the actual relationships between size and age at sexual maturity is still unclear although some physiologists, such as Alm (1959), believe that it is closely related to initial growth rate. Since little is known about the early life history of witch flounder in the Newfoundland-Labrador area, such relationships between maturity, size, and age are difficult to evaluate conclusively.

ACKNOWLEDGMENTS

The assistance of C. Butt who drafted all the illustrations is gratefully acknowledged.

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EARLY LIFE HISTORY OF SAND LANCE (*AMMODYTES*), WITH EVIDENCE FOR SPAWNING OF *A. DUBIUS* IN FORTUNE BAY, NEWFOUNDLAND

E. L. DALLEY AND G. H. WINTERS[1]

ABSTRACT

Ichthyoplankton surveys in Fortune Bay, Newfoundland, indicate that sand lance (Ammodytes sp.) larvae occur annually in Fortune Bay from February, when recently hatched yolk-sac larvae occur, until July/August when, it is assumed, the larvae have grown to the size of metamorphosis and have taken up a demersal existence. Length-frequency data indicate the spawning season to extend from December to May-June, and this extended spawning season probably accounts for the consistent polymodality in length-frequency distribution of sand lance larvae from the Newfoundland area.

Meristic development is shown to be complete by the time a length of 35-40 mm is reached and analyses of meristic counts indicate that the large (>20 mm) sand lance larvae caught in Fortune Bay belonged to the offshore species *Ammodytes dubius*. Further, analyses of pre-anal melanophore counts and oceanographic features of the area indicate that yolk-sac larvae taken in Fortune Bay in February were also *A. dubius*. This is the first record of the occurrence and spawning of *A. dubius* in coastal Newfoundland waters. This finding is significant in view of the current confusion regarding the appropriate taxonomy of sand lance populations in the Northwest Atlantic.

Sand lance, *Ammodytes* sp., are widely distributed in the Northwest Atlantic from Greenland south to Cape Hatteras, NC (Liem and Scott 1966). Although presently commercially unimportant, they hold a strategic niche as a major food organism for numerous commercial fish species, and Winters (1981, 1983) listed sand lance as a prey of haddock, Atlantic cod, silver hake, yellowtail flounder, American plaice, and Atlantic salmon. They are also fed heavily upon by certain large marine mammals (Overholtz and Nicolas 1979), and it has been postulated (Winters 1983) that their importance as a prey species is enhanced during times of low capelin abundance.

Taxonomy of the Northwest Atlantic sand lance has received considerable attention (Richards et al. 1963; Richards 1982; Scott 1968, 1972; Winters 1970). Generally two species are recognized in the Northwest Atlantic, i.e., *Ammodytes americanus* (=*Ammodytes hexapterus*), which is the deep-bodied, inshore form, and *Ammodytes dubius*, the slender-bodied, offshore form. Their taxonomy, generally, is confused by the presence of two clines in their meristic character frequencies: one north to south cline, the other inshore to offshore cline, with frequent overlap in the ranges of meristic numbers (Reay 1970). The validity of the two species is also questioned due to correlations of meristic numbers with environmental conditions (Scott 1972). In the Newfoundland area, however, the two species exhibit quite distinct meristic counts (Winters 1970). For the purposes of this paper we use the species classification of Liem and Scott (1966).

Winters (1970) has described the meristics and morphometrics of both species from the Newfoundland area and described *A. dubius* in the offshore and *A. americanus* inshore. Winters (1981, 1983) has described aspects of the biology of *A. dubius* from the Newfoundland Grand Banks. Little information exists on their early life history in the Newfoundland area. Dannevig (1918) provided length and distribution information for 89 specimens of sand lance captured off southern Newfoundland in surface and vertical hauls in early summer 1915. He assigned the specimens to *A. tobianus* (Linnaeus), a European inshore species. Frost (1938) presented information on the distribution of sand lance larvae around Newfoundland from 1931 to 1935. No size information was provided, and she assigned all the specimens from both near shore and the edge of the Grand Banks to *A. americanus*. In spite of its importance as a forage fish to commercially important species, no other information exists for sand lance larvae from the Newfoundland area.

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Information in the literature supports the hypothesis that the two species are allopatric. Winters (1970) found, based on adult samples, that *A. dubius* occurred exclusively in offshore areas and *A. americanus* exclusively in inshore bays around Newfoundland. Reay (1970) pointed out that *A. dubius* is exclusively an offshore species although Richards (1982) indicated that there are offshore components to *A. americanus* in the New England area. This paper presents information on sand lance in Fortune Bay, Newfoundland, as a further test of the hypothesis that the two species are allopatric. Size and distribution (seasonal and diurnal) information on *Ammodytes* larvae both within and at the mouth of Fortune Bay is presented as well as length-frequency information for other parts of the Newfoundland-Labrador area. The development of the definitive number of meristic characteristics is examined to identify the Fortune Bay larvae and, in conjunction with this, aspects of the developmental biology of *Ammodytes* sp. in the area are also described.

MATERIALS AND METHODS

Fortune Bay is a three still fjord located on the south coast of Newfoundland (Figs. 1, 2). Typically it has a two-layered structure with relatively warm (1.9°C) deep water in the outer portion in winter and cold (−0.25°-0.50°C) deep water in summer (de Young 1983). Annual surface temperatures typically range from 0.0°-1.0°C in February to 12°-16°C in August and September.

From June 1979 to February 1981, several ichthyoplankton surveys were carried out annually in Fortune Bay. The target species for the surveys was herring, *Clupea harengus*, but due to low numbers of herring larvae during the first three years the study was relocated, and during 1982-83 only one survey (July) was carried out in each year in Fortune Bay. Sand lance data examined here were collected during these surveys (1979-83).

Larvae collected in 1979-80 were taken by standard oblique plankton tows (Smith and Richardson 1977) using a 60 cm diameter bongo frame with 333 μm mesh netting on one side of the frame and 505 μm on the other. Tows were to a maximum depth of 200 m where possible. Nets were payed out at a speed of 0.77 m/second and retrieved at a speed of 0.38 m/second. After 1980 samples were caught in nets when both sides of the bongos were equipped with 333 μm netting.

In February 1981, collections were made using stepped oblique tows (5 minutes at each of 200, 150, 100, 50, 20, and 0 m) with a nonclosing N.I.O. rectangular midwater trawl (RMT-8) (Baker et al. 1973). During this survey all stations were fished during 6 hours of daylight with sets on the same stations being repeated after dark. A 10-min surface tow (3/4 m conical plankton net, 333 μm mesh) was carried out during each of the oblique tows with the RMT-8.

In June 1981, sand lance larvae were collected using bongo nets during the regular survey and also from special stations to investigate diurnal distribution. During each of these special stations, bongos were fished obliquely (to 200 m), and 3/4 m conical plankton nets (333 μm) were fished for 10 minutes at the surface during daylight hours and again (at the same positions) after dark of the same day.

Catches from all trips were preserved in a 5% formalin solution buffered with sodium borate. Fish larvae were later sorted, identified, counted, and measured. Total length was recorded to the nearest millimeter. A Macdonald and Pitcher (1979) mixture analysis was performed on the length-frequency distribution of the large sample from June 1979 to investigate the fit of the data to mixtures of normal distributions approximating the data.

Species designation was determined using meristic characters where possible (June 1979, June 1981), namely, vertebral, anal fin ray, and dorsal fin ray counts. Due to their small size, the specimens were stained for cartilage using Alcian blue and counterstained with alizarin red (Dingerkus and Uhler 1977). Counts were then done under a dissecting microscope (20-40× magnification) with the aid of the camera lucida.

Additional sand lance length-frequency data are presented, which have been on file at the Science Branch, Northwest Atlantic Fisheries Center in St. John's. These sand lance were collected incidentally during tows for other target species around Newfoundland using fishing and plankton gear (see Figures 1 and 4).

RESULTS

Seasonal and Diurnal Distribution

Table 1 lists the cruises in Fortune Bay from 1979 to 1983.

Sand lance larvae were encountered during 9 of the 17 cruises in Fortune Bay from 1979 to 1983

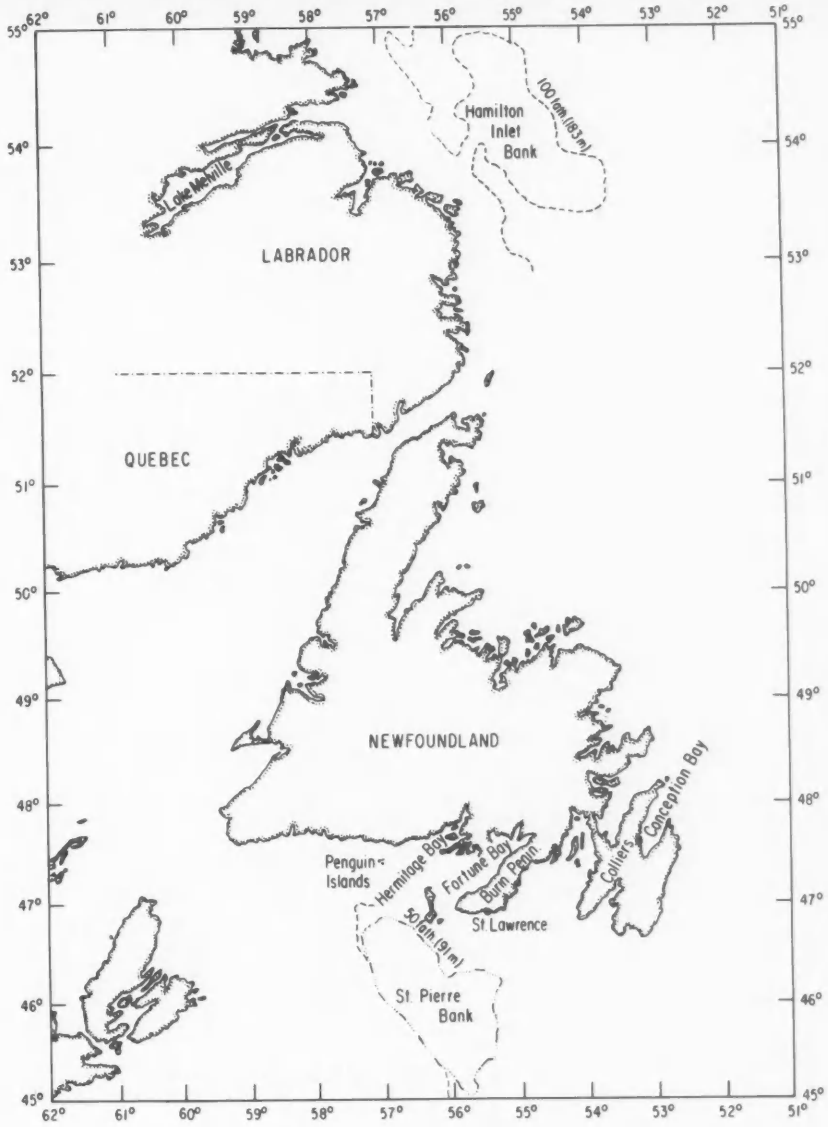


FIGURE 1.—Map of Newfoundland indicating places referred to in the text.

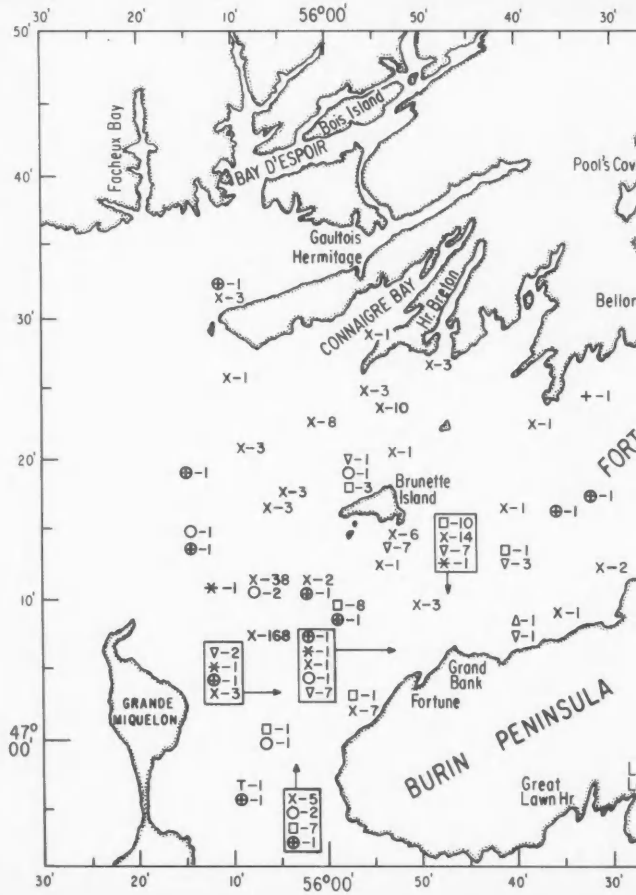
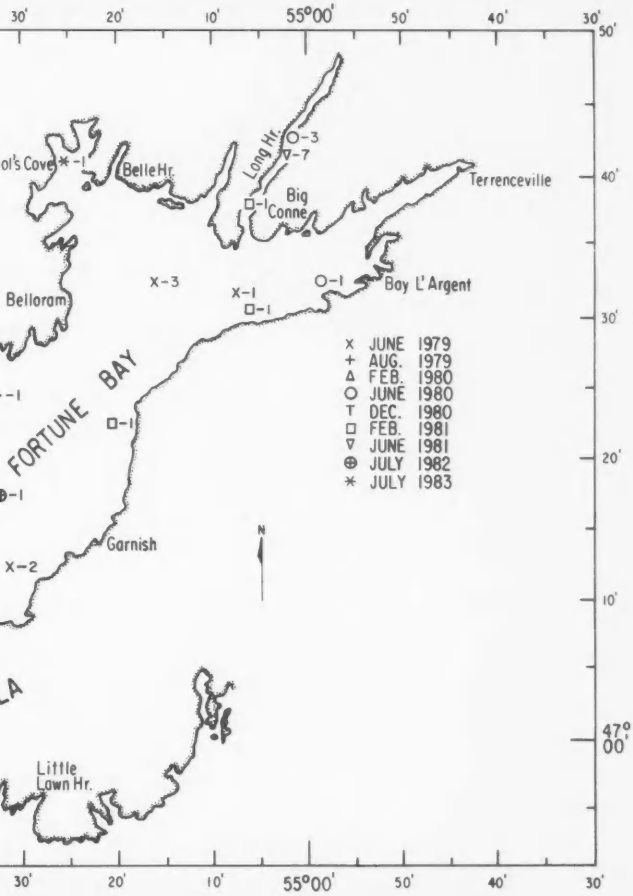


FIGURE 2.—Distribution and catch of *Ammodytes* larvae collected dur



ed during ichthyoplankton surveys in Fortune Bay from 1979 to 1983.

(Table 1), and the spatial distribution of these catches is shown in Figure 2. Sand lance larvae have a fairly wide distribution within and at the mouth of Fortune Bay; however, the incidence of positive catches and the size of the catches were greatest in the area between Miquelon and Fortune, north to Brunette Island.

The highest and most consistent catches of sand lance larvae were made in June and July, and only two specimens were caught in the August-November period. Yolk-sac larvae were taken only in surveys carried out in February, but larger larvae apparently remained in the water column until July-August at which time it is assumed that metamorphosis is complete, and the postlarvae take on a demersal existence. Macer (1966) gave the length of metamorphosis as 30-40 mm. Surveys in August of 3 consecutive years caught only one larva (43 mm), and surveys later than August caught only a single 82 mm postlarva in December 1980.

Catches of sand lance larvae from two periods in 1981 illustrate day-night variability in catches, especially at the surface (Table 2). During February, 44 stations were fished twice the same day, once during daylight and once after dark using stepped-oblique tows with the RMT-8 and surface tows with conical nets. Thirty-two larvae (94%) (mean length of 7.7 mm) were taken in night sets: 2 in oblique tows and 30 in surface tows. Of the two caught during daylight hours, one was in the surface tow and one in the oblique.

In June, 12 stations were fished using standard oblique tows with bongo nets and horizontal surface tows with conical nets during daylight and darkness of the same day. Twenty-five larvae

TABLE 1.—List of ichthyoplankton surveys carried out in Fortune Bay, Newfoundland, 1979-83, indicating gear fished, number of stations, numbers, and length information of *Ammodytes* sp. caught.

Cruise	Date	Gear[1]	No. stations fished during survey	No. positive sets	No. larvae caught	No. extra sets	No. positive catches (extra sets)	No. larvae in extra sets	Length range (mm) (all larvae)	Mean and SD of total length (mm)
Marinus 15	June 1979	B	71	28	302				10-43	22.9 (15.7)
Shamook 51	Aug. 1979	B	60	1	1					43.0
Marinus 21	Nov.-Dec. 1979	B	53							
Shamook 57	Feb. 1980	B, R	25, 25	1	1				8.0	
Marinus 25	June 1980	B	52	8	12				8-40	18.3 (9.5)
Marinus 28	Aug. 1980	B	42							
Shamook 64	Sept. 1980	R	50							
Shamook 67	Nov. 1980	B	48							
Shamook 69	Dec. 1980	B	52	1	1	[2]28B,28S				82.0
Shamook 71	Feb. 1981	R, S	44, 44	12	34				6-12	7.7 (1.0)
Shamook 76	June 1981	B	52	4	8	[2]24B,24S	8	27	12-61	38.4 (14.2)
Marinus 39	Aug. 1981	B	52			[2]22B,20R				
Shamook 79	Oct. 1981	B	52							
Shamook 81	Dec. 1981	R	35							
Shamook 82	Feb. 1981	R	29							
Shamook 88(2)	July 1982	B	52	11	11				14-46	22.1 (10.4)
Shamook 98(2)	July 1983	B	52	5	5				11-22	14.8 (4.2)

[1]B = BONGO, R = RMT-8, S = Surface net.
[2]Half of sets with each gear type during daylight; half at same station during darkness of same day.

TABLE 2.—Numbers of sand lance larvae caught in oblique[1] and surface tows during investigations into day-night catch variability, February-June 1981.

	Day				Night			
	February		June		February		June	
Type of tow	Oblique	Surface	Oblique	Surface	Oblique	Surface	Oblique	Surface
No. of sets	44	44	12	12	44	44	12	12
No. of positive catches	1	1	1	0	2	8	3	4
No. of Ammodytes larvae caught	1	1	2	0	2	30	9	16

[1]Oblique tow with RMT-8 in February, bongo in June.
[2]Includes 1 set at dusk in which 6 larvae were captured.

(93%) of 27 were taken in night sets: 16 at the surface and 9 in oblique tows. Two were caught in the oblique tows, and none, at the surface during daylight.

Size and Length-Frequency Distributions

Mean length data (Table 1) illustrate the annual variation in mean size during the late June-July period. In 1979, 1980, and 1982, the mean lengths of sand lance were 22.9 mm, 18.3 mm, and 22.1 mm, repectively. The 34 larvae caught in June 1981 were larger with a mean length of 38.4 mm, and the 5 caught in early July 1983 were smaller with a mean length of 14.8 mm.

Length-frequency distribution of the largest samples from Fortune Bay are shown in Figure 3. The distributions from June of each year indicate a wide range of lengths, and although samples from June of 1980 and 1981 are not large, the extended range in both suggests that the distribution is not unimodal and that there is more than one spawning cohort present. This extended length range may also result from delayed hatching or a combination of both these processes. In June 1979 there is a distinct mode at 23 mm with others probable at 14-15 mm and another at 29 mm. The length frequency of the June 1979 sample was subjected to modal analysis as described by MacDonald and Pitcher (1979). Three modes were interpreted from the length-frequency histogram. The results of the analysis indicated normal distributions with means at 13.4, 22.2, and 28.8 mm with standard deviations of 1.76, 3.02, and 4.36 mm, respectively (Table 3). The June 1981 sample of 33 larvae has a distinct mode at 45 mm, which is widely separated from a group of fish ranging in length from 12 to 17 mm. The wide range and polymodality in the length distributions of the June samples is good evidence of multiple spawning cohorts although differential hatching rates of the same cohort cannot be ruled out (S. Richards[2]). Given that sand lance larvae take 3-5 months (Reay 1970) to attain metamorphic sizes (30-40 mm, Macer 1966), the above observations suggest a spawning season extending from December through to April. In addition, the occurrence of larvae as small as 11 mm in July and 8 mm in June 1980 (Table 1) suggests that spawning may occur as late as May or June in certain years.

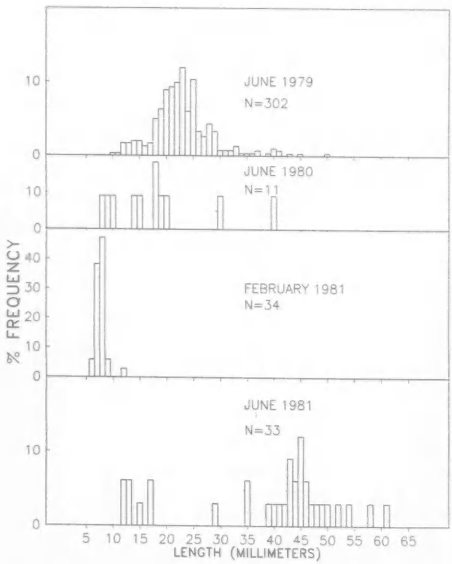


FIGURE 3.—Length-frequency distributions from Fortune Bay sand lance samples.

TABLE 3.—Results of the MacDonald and Pitcher (1979) method of analyzing length distribution mixtures of sand lance, June 1979, assuming a mixture of three (spawning) components. Results assuming only one component are also shown.

	Component	Percent of total population in component (SE)	Mean length (SE)	Standard deviation (SE)
$K = 3$	1	8.2 (2.9)	13.4 (0.77)	1.76 (0.52)
$\chi^2 = 25.32$	2	78.1 (28.2)	22.2 (0.65)	3.02 (0.53)
df 19				
$P = 0.1504$	3	13.7 (27.1)	28.8 (9.2)	4.36 (3.46)
$K = 1$				
$\chi^2 = 49.55$	1	100	22.4 (0.27)	4.65 (0.19)
df 25				
$P = 0.0024$				

This tendency for protracted length ranges is also evident in the historical samples collected around Newfoundland (Fig. 4). Samples are small, but the two from Labrador range in length from 22 to 55 mm with a break between the larger and smaller groups. The 14 fish from Colliers Bay, Conception Bay exhibit a protracted length range from 28 to 65 mm. The two samples collected off southern Newfoundland (Penguin Is-

[2]Sarah W. Richards, Little Harbor Laboratory, Inc., 69 Andrews Road, Guilford, CT 06437, pers. commun. October 1986.

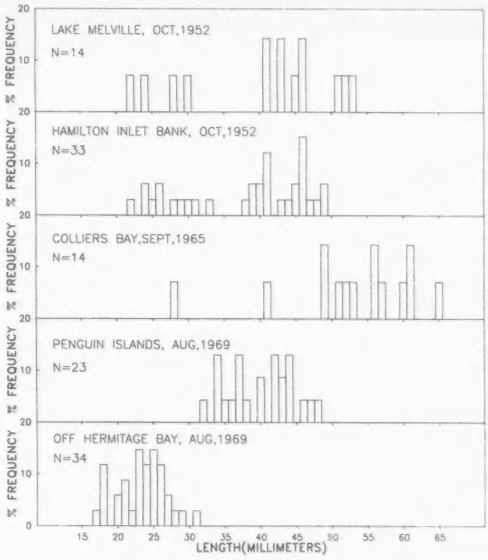


FIGURE 4.—Length-frequency distributions of historical sand lance samples from the Newfoundland area.

lands and Hermitage Bay) (Fig. 1) are interesting because although they were collected approximately 30 miles apart on successive days, the two samples have completely distinct length-frequency distributions. The sample collected on August 20 ranges in length from 32 to 48 mm, and the one collected on August 21 ranges from 17 to 31 mm. The distribution of both of these samples indicates that there may be more than one mode in each of the smaller and larger groups. These two completely different distributions may reflect multiple spawning cohorts or different spawning seasons in the case that they are comprised of different species.

Meristic Development

The staining procedure resulted in cartilaginous tissue being stained blue and ossified tissues red. Very few of the larvae had vertebral columns that stained for both cartilage and bone. The procedure resulted in three categories of vertebral columns. In the first category, the whole column stained blue, and this sometimes made counts difficult because parts of the notochord had not been replaced by individual vertebrae. The second category contained larvae in which part of the vertebral column was stained blue and part was stained red. These were few and had varying portions of red and blue stain. Neither the anterior nor the posterior portion of the vertebral column consistently ossified first. The third category contained those larvae in which all of the vertebral columns were ossified and stained red. Most larvae fell into this category. The observation that larvae in the second category did not show a consistent sequence of ossification may be an artifact of the preservation. Fixation of any protein or its amino acid derivatives will be followed by a drop in pH wherever formaldehyde is employed (Steedman 1976). Low pH causes decalcification or solubility of small deposits of calcium carbonate (Steedman and Omari 1976) and could therefore bias the interpretation of the normal developmental sequence of ossification. Moser (1972), Fritzsche and Johnson (1980), and Matarese et al. (1980) found that ossification of the vertebral column proceeded posteriorly in rockfish, white perch, striped bass, and Pacific tomcod, respectively. The sequence of development and ossification of fin rays was from anterior to posterior and from proximal to distal portions of the rays.

Table 4 and Figure 5 show the vertebral, dorsal fin ray, and anal fin ray counts for the length classes within the samples. The counts include both cartilageous and ossified fin rays. The full complement of dorsal fin rays is not developed until the larvae have attained a size of approximately 40 mm. The full complement of anal fin rays were developed by a size of 35-40 mm total length. Richards (1982) stated that fin ray development varied greatly in 21 specimens of both species but first appeared at 12-13 mm and was completely developed in 23 mm larvae of *A. americanus*. Fin rays first appeared at 14-15 mm in *A. dubius*, but the full complement was not present until after the larvae were greater than 25 mm total length. Scott (1972) found that the definitive number of anal fin rays were attained at a later stage in growth than 30 mm and that the definitive number of dorsal fin rays was attained at about 30 mm for Scotian Shelf *A. dubius*.

Figure 5 indicates that the definitive number of vertebrae is achieved by a total length of approximately 20 mm. As mentioned above, at sizes smaller than this, the notochord had not been replaced by vertebrae. This resulted in clear regions along the column. It was not possible to count myomeres because the staining process resulted in the fleshy parts of the body being cleared.

Matarese et al. (1980) pointed out that considerable variation occurs in the development of meristic structures of Pacific tomcod, *Microgadus proximus*, because the size at which bone ossifies varies from specimen to specimen. Figure 5 illustrates this variation in the mean counts of dorsal and anal fin rays at the smaller length classes.

Species Identification

Sand lance larvae collected in Fortune Bay in June 1979 had a mean vertebral count of 73.98 (SD = 1.66) (Table 4, Fig. 5). From Figure 5 and Table 4, the definitive number of dorsal fin rays varies from 64 to 68 with a mean of 65.53, and similarly the definitive number of anal fin rays varies from 32 to 36 with a mean of 34.09 (Table

TABLE 4.—Results of vertebral, dorsal fin ray, and anal fin ray counts for the length classes of sand lance.

Length class	*N*	Range	Standard deviation	Mean
Vertebrae				
22.5	49	72-76	0.90	73.98
27.5	75	71-76	1.14	73.95
32.5	19	73-77	1.10	74.11
37.5	8	73-75	0.76	74.00
42.5	13	72-75	1.09	73.77
47.5	5	73-77	1.67	74.40
52.5	4	72-75	1.26	73.75
>22.5	173	71-77	1.66	73.98
Dorsal fin rays				
22.5	69	22-45	3.66	30.04
27.5	69	28-47	3.93	35.72
32.5	16	39-65	9.27	49.31
37.5	5	44-66	9.63	61.20
42.5	10	64-68	1.27	65.50
47.5	5	65-67	1.10	65.80
52.5	4	64-67	1.26	65.25
>42.5	19	64-68	1.17	65.53
Anal fin rays				
22.5	67	25-33	1.79	30.66
27.5	72	27-35	1.20	32.17
32.5	18	31-35	1.13	32.89
37.5	6	33-36	1.17	34.17
42.5	8	33-36	1.06	34.38
47.5	4	33-35	0.96	34.25
52.5	4	32-34	0.96	33.25
>37.5	22	32-36	1.06	34.09

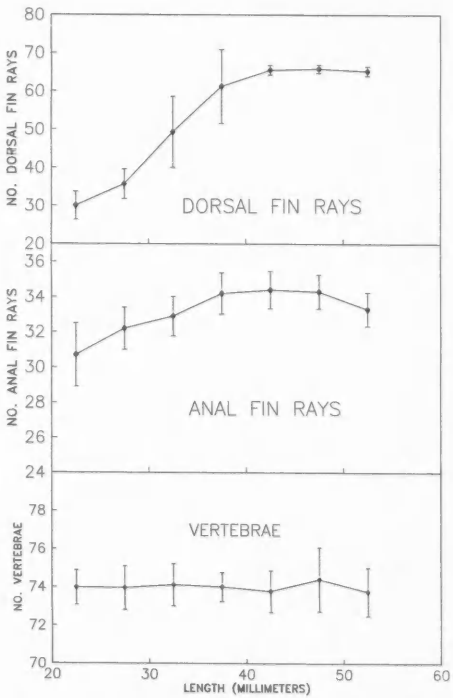


FIGURE 5.—Development of definitive number of dorsal fin rays, anal fin rays, and vertebrae with increasing size of sand lance, showing mean and standard deviation for each length class.

4). Winters (1970) gave mean vertebral counts of approximately 73.8-73.9, mean dorsal fin ray counts of 64.3-64.6, and mean anal fin ray counts of 33.2-33.6 for *A. dubius* from the Newfoundland Grand Banks. Comparable values for *A. americanus* from inshore areas of Newfoundland are 66.2-68.2, 55.7-57.8, and 27.8-30.6. We conclude, therefore, that the larger larvae collected in Fortune Bay in June 1979 belong to the offshore form, *A. dubius*.

The small larvae from February 1981 (lengths 6-12 mm) were examined for the presence of lateral or pre-anal melanophores. Counts of other melanophores (e.g., pectoral and subdorsal) were not possible, due either to the early stage of development of the larvae or to bleaching by the preservative. According to Richards (1982), counts of pre-anal melanophores can be used to distinguish between the larvae of *A. dubius* and *A. americanus*. From 6.0 to 8.9 mm in length, *A. americanus* has 0-16 pre-anal melanophores, and *A. dubius* has 10-21. Full or partial counts were possible for 11 of the larvae. Ten were 6-7 mm in length. Of these, two had 15 pre-anal melanophores, four had 16, one had 17, one had 18, and two had 20. One 9 mm larva had 15 pre-anal melanophores. According to Richards' (1982) criteria, four larvae are definately *A. dubius* because the counts are out of range for *A. americanus*. The other seven are in the upper extreme of the overlap range for the two species suggesting that these too are *A. dubius*. Thus, not only do larger larvae of the offshore species occupy Fortune Bay, but yolk-sac larvae are also present. This suggests that spawning of the offshore species occurs within the bay.

Because *A. dubius* is present on St. Pierre Bank (Winters 1970), we have considered the possibility that the yolk-sac larvae collected from Fortune Bay in February 1981 were transported from St. Pierre Bank. Smigielski et al. (1984) gave times for yolk-sac absorption from 5 to 14 days, depending on temperature. Using minimum and maximum speeds (0.05-0.20 ms^{-1}) of the Labrador Current along the south coast of Newfoundland (Petrie and Anderson 1983), it would take yolk-sac larvae 9-36 days to be carried from St. Pierre Bank to inner stations in Fortune Bay where they were collected. De Young (1983), however, described a seasonal cycle of water exchange for Fortune Bay in which the flow of Labrador Current water over St. Pierre sill (between Miquelon and the tip of the Burin Peninsula (Fig. 2)) is minimal in winter months and predominates in the summer. Under normal current conditions, it appears unlikely that these yolk-sac larvae were transported over St. Pierre Bank into Fortune Bay with the Labrador Current during the winter period. A persistent wind event from the south could transport larvae in the surface layers at a much faster rate than would the inshore branch of the Labrador Current. However, the prevailing wind direction at St. Lawrence on the southern part of the Burin Peninsula for January and February 1981 was from the west with wind from the south only 1% of the time in January and 6% in February 1981 (Anonymous 1981). A peak wind event from the SSE on February 9 did not persist into the next day when winds were again from the west. We conclude, therefore, that it is unlikely that the yolk-sac larvae found within Fortune Bay in February 1981 were transported from St. Pierre Bank. More likely, these larvae were spawned in Fortune Bay. Such spawning is consistent with evidence from hydrographic charts that indicate many areas of gravel and sand mixtures in Fortune Bay. According to Reay (1970), this is the preferred spawning substrate for sand launce.

Yolk-Sac Absorption

Sixty-two percent of the larvae collected in February 1981 contained yolk sacs. The mean length of those in which the absorption of yolk-sac (+ oil globule) was complete was 8.1 mm while those with absorption incomplete had a mean length of 7.4 mm. This is consistent with published records. Smigielski et al. (1984) gave yolk-sac absorption lengths of 7.2-7.41 for laboratory reared *A. americanus*, and Richards (1965) found that oil globule absorption was complete between 5 and 7.5 mm.

DISCUSSION AND CONCLUSIONS

The conclusion from the data collected during the day-night investigations is that smaller yolk-sac larvae in February and larger larvae in June are more abundant or more available to the gear at night. It is difficult to discern a particular pattern of diurnal and vertical migratory behavior for sand lance larvae from the literature because documentation on the subject has not been consistent. The observation that larger larvae in June are more abundant at night is not unusual and may be attributable to net avoidance (Norcross et al. 1961; Richards and Kendall 1973; Potter and Lough 1986). The observation that yolk-sac lar-

vae are more abundant in surface night sets appears unusual since Richards and Kendall (1973) found that in winter larvae 8-17 mm were more abundant in deep tows at night and surface tows during the day. Avoidance behavior does not appear to develop until a size of greater than 10 mm (Norcross et al. 1961; Potter and Lough in press). Assuming the same for larvae in Fortune Bay, it is not likely that yolk-sac larvae were avoiding the gear during the day. Although it is not possible to make a definite conclusion on vertical migration with the relatively small number of larvae, the data suggest that yolk-sac larvae in February are also capable of vertical migration.

Our analyses of sand lance larvae from Fortune Bay have demonstrated for the first time the occurrence and probable spawning of the slender-bodied *A. dubius* in coastal waters in Newfoundland. Previous studies by Winters (1970) have indicated the occurrence of only the deep-bodied form *A. americanus* in Newfoundland bays with *A. dubius* being found exclusively on the offshore banks. This finding is significant in light of the current confusion as to the appropriate taxonomy of the sand lance populations in the Northwest Atlantic. Both *A. americanus* and *A. dubius appear to* resemble *A. marinus* which is currently considered to occur only in European waters (Reay 1970), and the characteristics used to separate the two Northwest Atlantic types from each other and from *A. marinus* are sometimes tenuous particularly in southern parts of the range. In the Newfoundland area, however, *A. americanus* and *A. dubius* maintain distinct meristic counts. The occurrence and probable spawning of *A. dubius* in a coastal area, formerly considered to be inhabited exclusively by *A. americanus* (Winters 1970), indicates sympatry. This provides evidence that the two forms are reproductively isolated and therefore separate species. This is substantiated by the fact that the meristics described for *A. dubius* larvae in Fortune Bay and those offshore (Winters 1970) are identical.

We have also demonstrated that the spawning season of sand lance in Fortune Bay, Newfoundland, is protracted and probably extends from December to May or June. This spawning period is much longer than in southern areas of the Northwest Atlantic where the spawning season in inshore waters is from the period December to February (Richards 1982). It is possible that this extended spawning season is also a result of the mixture of the two species in Fortune Bay; however, the polymodality in the length frequency of large *A. dubius* (>20 mm) larvae in Fortune Bay suggests that an extended spawning season may be characteristic of this species in coastal Newfoundland waters.

ACKNOWLEDGMENTS

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NOTES

HEART AND GILL VENTILATORY ACTIVITY IN THE LOBSTER, *HOMARUS AMERICANUS*, AT VARIOUS TEMPERATURES

Heart rate and gill ventilatory activity have been suggested as useful measures of the physiological condition of decapod crustaceans and their response to various environmental conditions. Several authors have described altered ventilatory and heart rates in response to such variables as temperature, salinity, and dissolved oxygen (Uglow 1973; Cumberlidge and Uglow 1977; Taylor 1977; Hagerman and Uglow 1979). Price and Uglow (1980) also discussed the applicability of these measures in studies of pollutant stress where they described the effects of copper, cadmium, and zinc on the heart and ventilatory rates of *Crangon crangon*. The mechanics of ventilatory reversals of decapod crustaceans have also been described; for example, the reverse ventilatory pulses (coughs) produced by the American lobster, *Homarus americanus*, during a muscular compression of the branchial chamber probably provide irrigation to the posterior area of the gills or help to clear detritus from gill surfaces (Wilkins and McMahon 1972; Bill and Thurberg 1985). The frequency of the lobster cough response increases after exposure to a variety of waterborne chemicals, and it has been suggested that this response might be a useful measure for detecting aquatic pollutants (Bill and Thurberg 1983, 1985). Before these heart and ventilatory measures can be employed as monitoring tools, however, baseline information should be collected on their seasonal variability under normal, unpolluted conditions, against which to interpret any stress-induced change. This study addresses the relationship between heart, gill-bailer, cough rate, and seasonal water temperature.

Methods

Adult American lobsters (61.4-91.2 cm carapace length) were trawl-collected in Long Island Sound off Milford, CT, and held in running seawater at ambient temperature. Seawater for this building is taken from Milford Harbor, a harbor with good tidal flushing and no industrial development. The pollutant content here is very low; for example, seawater cadmium is <0.5 ppb, mercury <1 ppb, lead <5 ppb, and copper 2-4 ppb. The PCB levels (0.67 ppm, wet weight) in blue mussels, *Mytilus edulis*, from Milford Harbor are typical of levels found in molluscs along the U.S. east coast (Farrington et al. 1983; Greig and Sennefelder 1985). Although no area of Long Island Sound can be considered "pristine", this area has excellent water quality for holding and rearing marine animals as evidenced by a 50-yr laboratory history of marine invertebrate culture. The salinity range is 26-28 ppt with occasional brief low salinity episodes during extreme rains (not during this study, however) and the dissolved oxygen levels remain at or near saturation at the temperatures in this study. The lobsters were fed chopped clams, fish, or crabs daily. Heart, gill-bailer, and cough rates were monitored with 6 mm silver disc electrodes, an impedance converter, and an amplified polygraph recorder, following the methods described in Bill and Thurberg (1985). Measurements were made at 2°, 6°, 10°, 14°, and 18°C over a 1-yr period. Each lobster was allowed to acclimate to temperature for at least 2 weeks before testing. Between 9 and 23 lobsters were monitored at each temperature for a 1-h period. Rates were calculated on a per-minute basis.

Results and Discussion

Crustacean metabolism varies with temperature (Wolvekamp and Waterman 1960; Taylor et al. 1977, 1973). Aiken (1980) observed that elevated temperatures accelerate the metabolic processes in lobsters, although the parameters were not defined. The data presented here confirm this increase in metabolism using three physiological parameters. Figure 1 shows the increasing frequency of heart and gill-bailer rates as the temperature rose from 2° to 18°C. Cough rate also increased with increasing temperatures (Fig. 2). Bill and Thurberg (1983) reported a cough rate of 0.4 coughs/minute at 10°C in this species, a rate similar to that reported in this study at 10°C (0.32 coughs/minute). The data reported here present a full seasonal profile of three important metabolic measures. They provide a

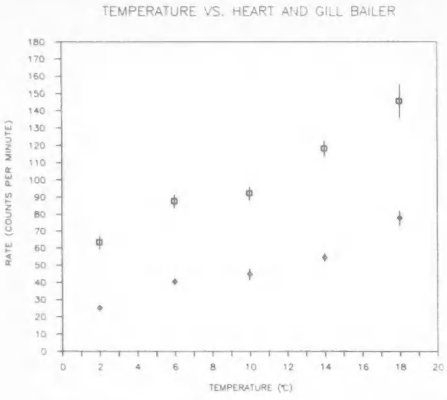

FIGURE 1.—Temperature (°C) versus heart (◇ and gill bailer (□) rate (counts per minute) of the American lobster, *Homarus americanus*, at 2°, 6°, 10°, 14°, and 18°C. Each point is the mean value of 9-23 lobsters and the vertical line is ±1 standard error.

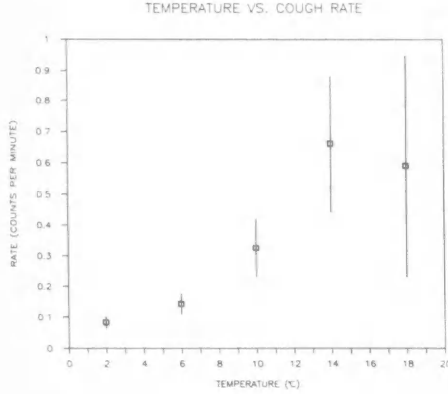

FIGURE 2.—Temperature (°C) versus cough (□) rate (counts per minute) of the American lobster, *Homarus americanus*, at 2°, 6°, 10°, 14°, and 18°C. Each point is the mean value of 9-23 lobsters and the vertical line is ±1 standard error.

comprehensive and easy-to-interpret baseline against which to compare similar measures made on lobsters from areas suspected of pollutant impact.

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A METHOD OF SIMULTANEOUSLY TAGGING LARGE OCEANIC FISH AND INJECTING THEM WITH TETRACYCLINE

A simple method of marking large oceanic fish such as yellowfin tuna, *Thunnus albacares*, and wahoo, *Acanthocybium solandri*, for age determination studies is described. The method, developed for tagging and injection with tetracycline of yellowfin tuna >45 kg from the deck of sport fishing vessels, is easily adaptable to other species, including billfish and possibly marine mammals.

The use of calcium-specific markers, such as oxytetracycline (OTC), to validate the temporal significance of natural marks in hard parts has become increasingly widespread. Validation is recognized as a basic requirement of age and growth studies (Beamish and McFarlane 1983). OTC is usually administered orally, intraperitoneally, or intramuscularly (Weber and Ridgway 1967; Wild and Foreman 1980; Campana and Neilson 1982). Boating and restraining while OTC is injected causes stress and trauma to the fish and may result in injury to the tagger when large, powerful pelagic fish are tagged. Nevertheless, biologists from the Inter-American Tropical Tuna Commission (IATTC) have successfully tagged and injected medium-sized (up to 36 kg) yellowfin tuna (Anonymous 1982) where, using multiple poles (two pole method, described in Godsil 1938), the crew pulled the fish onto the padded aft deck (Bayliff and Holland 1986) of a dedicated tuna baitboat. Although this method would probably suffice when tagging even larger fish, dedicated vessels are costly and there is no guarantee of locating adequate-sized fish during the charter period. Opportunistic tagging by the crews of long-range sportfishing boats, which frequently capture large tuna but lack gear to handle live fish on deck, was an attractive prospect.

Methods and Materials

A device used for administering drugs to zoo animals (Extend-O-Jector[1], model A, Kay Research Products, Hyde Park Bank Bldg., Suite 503, 1525 East 53rd St., Chicago, IL 60605 USA) was modified (Fig. 1) by adding a stainless steel dart tag applicator held at an appropriate distance with 13 mm thick PVC sheet press-fitted to the distal end of the injector head. The applicator was then fastened to the grooved base of the injector head with a hose clamp, stabilizing it during use. Other types of applicators, such as those used for metal anchor tags (Bayliff and Holland 1986) can be easily substituted. Depending on the tag type, a rubber band may be used to hold the tag in place during application.

The device utilizes either a 3 to 5 cc disposable syringe and a 2-in (51 mm) needle. For tunas, a 17 gauge needle provided the best combination of sufficiently high delivery rate and minimum puncture diameter.

As the decks of most long-range sportfishing boats are quite far off the water (2 m), the device was bolted inside a 25 mm ID telescoping tubular aluminum pole, the type normally used with swimming pool cleaning equipment. The length may then be adjusted to suit individual situations.

When a large tuna was captured by an angler, the tag and injection was administered below the second dorsal fin while the fish was still in the water. Through trial and error, application was found most efficient when the device is continuously pushed toward the fish's body after initial insertion of the applicator needles. Best results are obtained when the device is kept as near to perpendicular to the body of the fish as possible, preventing the needles from bending, damaging the fish, or both. The fish is released by removing the hook by jerking the bend of the hook with a gaff forwards while pulling the line backwards, or cutting the leader as close to the hook as possible. Under certain conditions, free-swimming fish found at the surface may be tagged and injected.

A previous experiment (unpubl. data, Inter-American Tropical Tuna Commission, La Jolla, CA) determined that doses as low as 10 mg/kg body weight formed readable marks in the vertebrae of mackerel, *Scomber japonicus*. Wild and Foreman (1980) and Foreman (1987) determined that a dosage of 27 mg OTC/kg body weight formed a brilliant mark in the otoliths of yellowfin and skipjack, *Katsuwonus pelamis*, tunas and in otoliths and vertebrae of bluefin tuna, *Thunnus thynnus*. For large fish (near 45 kg), the volume required using standard veterinary injectable (100 mg/mL) OTC would be unmanageable; a more concentrated form (200 mg/mL; Pfizer Liquamycin LA-200) was substituted. Because the marks formed in smaller fish were sufficiently bright, the dose was reduced by half, to about 13.5 mg/kg.

[1]Reference to trade names does not imply endorsement by the National Marine Fishers Service, NOAA.

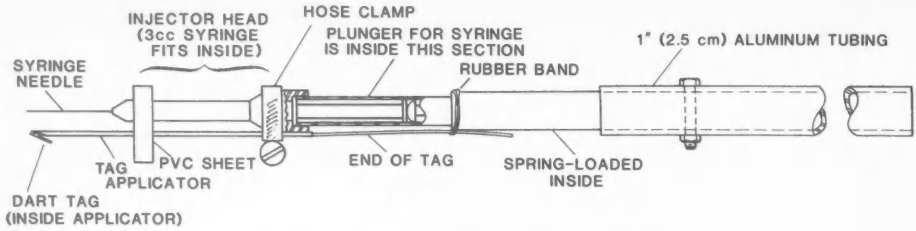

FIGURE 1.—A tag and injection device for large pelagic fish.

Results and Discussion

On the night of 27-28 January 1986, the crew and passengers of a 34 m long-range sportfishing boat, *Royal Polaris*, tagged, injected, and released 36 yellowfin tuna, all estimated to be >45 kg. Six of these fish were recaptured from 14 to 83 days later, indicating that the tagged fish were active and feeding.

Differences in return rates between this method and the padded deck method (Table 1) are possibly due to such factors as differences in size and age of the fish tagged, fishing effort in the tagging area, or the amount of stress caused by different fishing methods, rather than some characteristic of the pole method.

The otoliths from recaptured fish displayed the yellow-green fluorescent mark when viewed under ultraviolet light, but the marks appeared much fainter than those on otoliths returned from the program which used a padded deck. Since the dosage each fish received was monitored by the amount (if any) left in the syringe after application, failure of the device to deliver the full amount of OTC was ruled out. Similarly, the needle size was nearly the same for both treatments, and pore seepage is assumed equal. There were, however, differences in the type of OTC used. Liquamycin LA-200, used with the pole device, was found to contain a slow-release agent (2-pyrrolidone) which extends the antibiotic effect over time. Evidently the agent also slows deposition of the fluorophors such that their concentration in the area of osteogenesis and hence the brilliance of the mark is diminished. I recommend that an OTC solution without slow-release agents be used, e.g., Anchor Oxy-Tet 100, as in previous experiments.

TABLE 1.—Comparison of tag return rates from the padded deck method (unpubl. data, Inter-American Tropical Tuna Commission, La Jolla, CA) and pole injection device method for yellowfin >100 cm (20.5 kg) at release.

	Releases	Returns	Percent
Padded deck	49	16	32.7
Pole device	36	6	16.7

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SECOND RECORD OF THE KAWAKAWA, *EUTHYNNUS AFFINIS*, FROM THE EASTERN PACIFIC OCEAN

Although the kawakawa, *Euthynnus affinis* (Cantor 1849), is widely distributed throughout the warm waters of the Indo-West Pacific (Yoshida 1979), it is replaced by the black skipjack, *E. lineatus* Kishinouye, in the eastern Pacific. There is only one previous record of *E. affinis* in the eastern Pacific. That specimen, 361 mm fork length (FL), was reported from Los Angeles Harbor, CA, in 1952 (Fitch 1953). The second documented occurrence of *E. affinis* from the waters of the eastern Pacific is recorded in this note.

The specimen, *E. affinis*, 920 mm FL and 13.15 kg, was caught by Ronald Nakamura using hook and line from the long-range San Diego-based sport-fishing boat, *Royal Polaris*, on 17 December 1986, off Clarion Island (lat. 18°22'N, long. 114°44'W) in the Revillagigedo group. The specimen has been deposited in the Scripps Institution of Oceanography fish collection (SIO 87-70).

The morphometric and meristic characters for the specimen are given in Table. 1. The measurements were taken according to the methods of Godsil and Byers (1944) and Gibbs and Collette (1967). The external characters of this specimen agree with Godsil's (1954a) description of the species. The wavy oblique markings on each side of the dorsal surface, no dip in the lateral line below the second dorsal fin, and the several black to gray spots scattered over a relatively wide area between the pectoral and pelvic fins are characteristic of most specimens of this species. Furthermore, the morphometrics for this specimen are within the ranges for those body proportions reported by Godsil (1954b) and are closer to the morphometrics for *E. affinis* from Hawaii, rather than from Japan.

The internal characters also appear to agree with Godsil's (1954a) description of the species. High-quality radiographs produced by computer-assisted tomography (C.A.T.) scanning equipment were utilized for examing skeletal characters. The vertebral count is 20 + 19 = 39, and the radiographs showed no bony protuberances on any of the caudal vertebrae. However, no vomerine teeth were present. Although there was no indication of their previous presence, their absence could be explained by wear in this presumably old specimen. Nevertheless, the primary characters distinctive of *E. affinis*, 39 vertebrae, the total gill raker count of 31, and the absence of bony protuberances on the caudal vertebrae, leave no doubt on the identity of this specimen.

The occurrence of *E. affinis*, as well as the first documented occurrence of this specimen in the eastern Pacific, should be considered extremely rare events. No specimens of *E. affinis* were noted, during 1980-82 while personally examining a few thousand specimens of *E. lineatus* landed by commercial tuna vessels operating in the eastern Pacific. One of the remarkable fea-

TABLE 1.—Summary of morphometric and meristic data. The measurements are in millimeters.

Character	Measurements (mm)
Fork length	920
Head length	263
Snout-first dorsal	301
Snout-second dorsal	552
Snout-anal	590
Snout-ventral	291
Max. body depth	232
Max. body width	156
First dorsal-ventral	225
First dorsal-anal	385
Ventral-vent	310
Base first dorsal	238
Base second dorsal	72
Base anal	61
Pectoral length	138
Anal length	65
Diameter of iris	29
Maxilla length	97
Snout-posterior of eye	106
	Counts
Dorsal spines	15
Second dorsal rays	13
Dorsal finlets	8
Anal rays	14
Anal finlets	7
Pectoral rays	26
Gill rakers	8 + 1 + 22 = 31

tures of *E. affinis* is its extremely large size, particularly its weight of 13.15 kg, as this specimen represents the heaviest *E. affinis* documented. The previous documented record of maximum size for *E. affinis* was 11.79 kg based upon a specimen captured in Merimbula, NSW, Australia in 1980 (Anonymous 1986).

It is interesting that the maximum size records established for the black skipjack, *E. lineatus*, and the yellowfin tuna, *Thunnus albacares*, are based upon sport-caught specimens from the Revillagigedo group of islands. The fact that many species tend to be longer lived and reach maximum sizes in the northern latitudinal ranges of their distributions, apparently pertains to the aforementioned species of tunas, as well. In the case of this record specimen of *E. affinis*, although found outside its normal geographical distribution, the maximum size was attained in this same region of the Pacific Ocean.

Acknowledgments

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CONTRIBUTION TO THE LIFE HISTORY AND REPRODUCTIVE BIOLOGY OF GAG, *MYCTEROPERCA MICROLEPIS* (SERRANIDAE), IN THE SOUTH ATLANTIC BIGHT[1]

The gag, *Myceteroperca microlepis*, is a demersal serranid found along the southeastern coast of the United States and in the Gulf of Mexico (Smith 1971; Fischer 1978). Throughout its range the gag is of both commercial and recreational importance. Because of its relatively slow growth rate (Manooch and Haimovici 1978) and desirability, overfishing is of wide concern.

The gag is a protogynous hermaphrodite, and McErlean and Smith (1964) suggested that sexual transformation occurs during the 10th or 11th year. Spawning occurs from January to March off the west coast of Florida (McErlean 1963), and the maximum reported age is 13 years in both the Gulf of Mexico (McErlean 1963) and the South Atlantic Bight (SAB) (Manooch and Haimovici 1978). Microscopic examination of the gonads is necessary for definite sexual identification, but gonad morphology has not been specifically described. The purpose of this study is to provide new information on the age, growth, and reproductive biology of this important species, including a description of the morphology of gag ovaries and testes.

Methods

Most samples were obtained from the commercial hook and line fishery, and others were collected on research cruises aboard the RV *Dolphin*, RV *Oregon*, and RV *Lady Lisa* from 1976 to 1982. Specimens were measured (total and standard lengths), weighed, and sagittae removed from the otic capsule through the branchial chamber. Otoliths were stored dry and later viewed in a dish of cedar wood oil with reflected light over a dark background using a binocular microscope. Since opaque bands in larger otoliths were thin and often too crowded near the edge to permit accurate counting, cross sections (approximately 0.5 mm thick) were made on the dorsoventral plane of the otoliths through the center with a diamond dicing wheel mounted on an ISOMET[2] low speed saw. Sectioned otoliths were viewed in

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

the same manner as whole otoliths. If two readings by a single observer did not agree, otoliths were deleted from analyses. Additional verification of counts was then obtained from a second observer who read 200 otoliths (35%) selected randomly.

Because monthly samples did not contain similar porportions of large and small fish, calculations of monthly mean marginal increments of sagittae were biased. For instance, if primarily small fish are sampled in one month followed by mostly large fish in the next month, the mean marginal increment will decrease regardless of the time of year. To alleviate this bias, marginal increments were standardized by converting each measurement to a proportion of the maximum recorded for that age group. Thus, a measurement of 2.5 ocular units in an age group for which the maximum is 10.0 becomes equivalent to a measurement of 0.5 ocular units in an older group for which the maximum is 2.0.

Sex and reproductive conditions were determined from histological sections of gonads, which were preserved in 10% formalin, and later processed through an Autotechnicon Duo Model 2A automatic tissue processor, then embedded in paraffin, and sectioned with a rotary microtome at approximately 7 μm (Humason 1972). Tissues were then stained with Harris' hematoxylin and counterstained with eosin-Y. Sexes were identified as male, female, and hermaphroditic female or "transitional" (gonad primarily ovarian, with some traces of active testicular tissue present). Maturity was described following the synopses listed in Waltz et al. (1982). Terminology used in histological descriptions follow Hyder (1969), Combs (1969), and Wallace and Selman (1981).

Results

A total of 1,039 gag ranging in total length (TL) from 153 to 1,150 mm was examined for life history information. Of the 652 otoliths on which age determinations were attempted, 87% showed discernible rings verified by two readings. No otoliths were deleted from analyses because of disagreement between primary and secondary readers. Marginal increment measurements from the outer edge of the last opaque band to the dorsal margin of whole sagittae indicate that these bands are laid down in late spring to midsummer. Bands are apparently laid down earlier and over a longer time period (May-August) in ages ≤VIII than in older gag. Although sample sizes of fish ≥age IX on which marginal increments were measured are small in relation to those of younger gag, it appears that ring formation is concentrated in August (Fig. 1). Twenty-two age groups were identified (Table 1).

The gag ovary is a hollow, bilobed organ suspended in the posterior region of the body cavity from the swimbladder by mesenteries. Blood vessels and nerves enter the gonad at the anterior point of each lobe's suspension and course medially to the mesenteries along the dorsomedial surface of each lob. The lobes fuse posteriorly, their

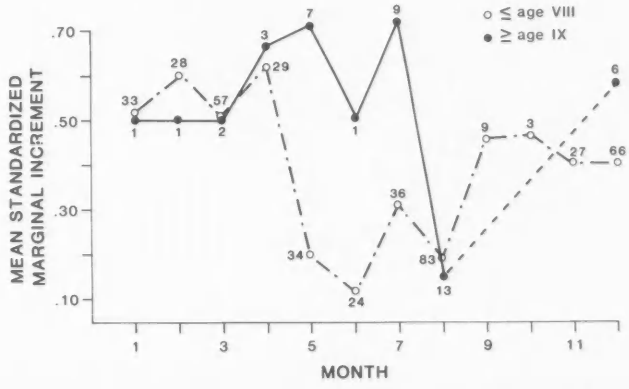

FIGURE 1.—Mean standardized marginal increments by month for gag ≤age VIII and ≥age IX, and sizes of monthly samples.

TABLE 1.—Observed mean lengths (mm), weights (kg), and sample size by age for *Mycteroperca microlepis*.

Age	Number	Total length (mm)	Standard length (mm)	Weight (kg)
0	14	187	153	0.087
1	17	347	293	0.605
2	18	466	383	1.263
3	26	575	470	2.104
4	49	677	555	3.881
5	80	767	641	5.558
6	102	824	686	6.040
7	91	865	729	7.612
8	51	895	751	8.454
9	21	936	789	9.810
10	19	959	807	10.491
11	23	993	826	11.399
12	7	1,004	841	13.327
13	4	1,048	884	14.950
14	2	1,066	905	13.000
15	2	1,096	927	14.748
16	9	1,064	905	14.495
17	10	1,076	904	14.767
18	10	1,068	887	14.310
19	5	1,087	924	14.074
20	5	1,071	896	15.150
21	1	1,125	950	15.400
22	1	1,124	946	—

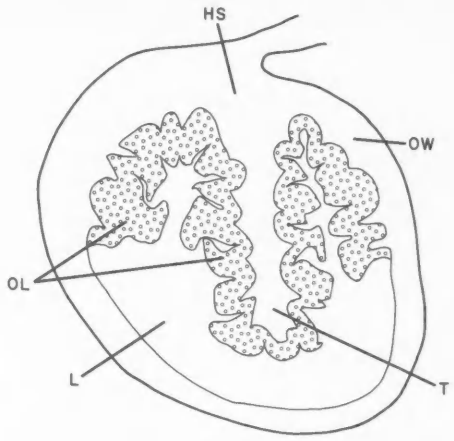

FIGURE 2.—Schematic representation of a cross-sectioned gag ovary (diameter = 3 cm). HS = halar stroma, L = lumen, OL = ovarian lamellae, OW = ovarian wall, T = "Typhlosole-type" invagination of the dorsal wall.

lumena forming a common oviduct. The lumena are incompletely lined with folded germinal epithelium (ovarian lamellae) within which oocytes develop and mature. The ventral regions of the lumena remain void of lamellae, and these alamellar areas are contiguous with the alamellar oviduct. In addition to the dorsal and lateral walls of the lumena showing lamellar development, there is a "typhlosole-type" continuation of the dorsal gonad wall projecting into each lumen. This projection of connective tissues into the center of the lumen apparently allows additional surface area for attachment of ovarian lamellae (Fig. 2).

During the sexual transition phase, testicular growth fills the existing ovarian lamellae, displacing and possibly dislodging the already degenerating oocytes. Transitional gonads were rarely found, and there were no cases of simultaneous development of gonad tissues. Male gonads retain the somatic morphology of the ovary. Testicular tissue is arranged in "false lamellae", primarily suspended from the "typhlosole-type" structure. Sperm sinuses form peripherally in what was previously the ovarian wall and continue posteriorly becoming the vas deferens within the oviduct wall. The vestigial ovarian lumena and oviduct remained in all testes examined. All testes also possessed many residual oocytes, some as large as 500 μm in diameter.

Females made up 84% of the gag which were sexed. Examining the percentage in each age class, we found that 28% of age III, 51% of age IV, and all older female gag had mature ovaries. Immature gag ranged from 290 to 680 mm TL, whereas the smallest mature female was 600 mm TL. Male gag accounted for 15% of the animals sexed and were found in ages V through XX (no sex available for age XXI and XXII fish). No males were found smaller than 790 mm TL (Fig. 3) and no juvenile males were found. Gag with transitional gonads made up 1.25% of all the groupers sexed and occurred in ages V through XI. The size range for fish undergoing sex succession was from 750 to 950 mm TL (Fig. 3).

The gag spawns once a year in late winter-early spring. Analysis of the relative abundance of developing, ripe, and postspawned gonads indicated that peak spawning activity was reached in late March and early April (Fig. 4) in the SAB.

Discussion

Use of whole sagittae in aging gag has been validated (McErlean 1963), and Matheson et al. (1986) successfully validated the use of sectioned sagittae to age the congeneric scamp, *Mycteroperca phenax*. These studies together with the present data provide good evidence that sagittal

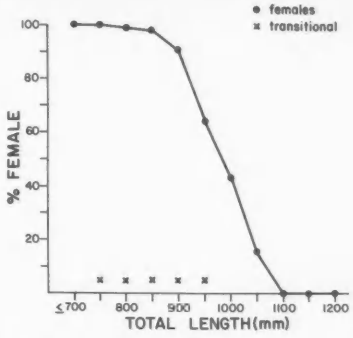

FIGURE 3.—Percent female gag by length class, and occurrence of transitional gag.

rings detected in the present study are annual in nature. While the importance of adequate validation has been well documented (Beamish and McFarlane 1983), it has become increasingly clear that annulus formation in many species can take place over an extended period, making it difficult to pinpoint this event in time. Peak annulus formation covered a 3-mo period for the groupers *Epinephelus drummondhayi* (speckled hind) and *E. niveatus* (snowy grouper) (Matheson and Huntsman 1984). Thus, the May-August period of peak ring formation for younger gag in the present study is not unusually long. Reasons for differences between ages ≤VIII and ≥IX in timing of peak annulus formation are not apparent. However, that the differences are at least partially based on sex is probable since the younger fish are predominately female while approximately 60% of the older group are male. A comparison strictly between sexes was not possible since samples of males available for measurement were obtained in only 5 months.

The use of sectioned sagittae greatly enhanced clarity among the higher age groups and allowed for greater distinction between rings in comparison to whole otoliths. Beamish (1979) found that sectioned otoliths of the Pacific hake, *Merluccius productus*, gave a more accurate account of age, especially when thick otoliths with poorly defined annuli were encountered. This appears to be true for the gag, as well. Twenty-two age groups were distinguished in the present study, similar to the 21 age groups reported for the scamp (Matheson et al. 1986), compared with previous reports of 13 age groups for the gag (McErlean 1963; Manooch and Haimovici 1978). The nine groups not detected previously do not represent just an increase in the percentage of readable otoliths (present study: 87%; McErlean 1963: 87%; Manooch and Haimovici 1978: 79%). Rather, it appears that additional annuli are present in the otoliths of the larger size classes that were not detected in previous studies using whole otoliths. For instance, the oldest fish collected by Manooch and Haimovici (1978) was age XIII and 1,201 mm TL, longer than any gag aged in the present study and 77 mm longer than the age XXII fish (Table 1).

Moe (1969) described the reproductive biology of the red grouper, *Epinephelus morio*, and many aspects of the development and sex succession schedules are similar to those found in the gag.

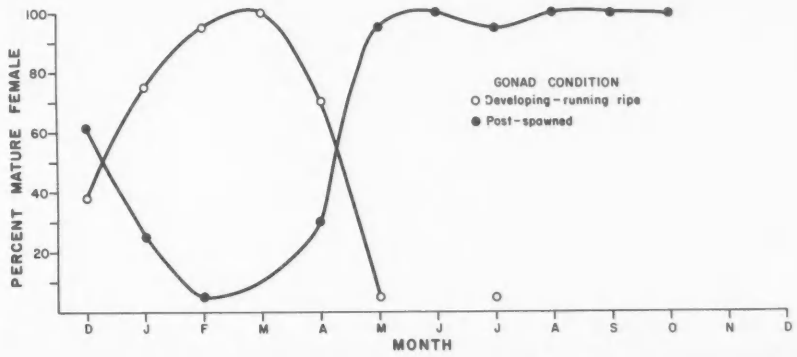

FIGURE 4.—Maturity stages of female gag by month of capture, illustrating the late winter-early spring spawning season.

The actual morphology of the gonad, however, differs from that described for red grouper. Moe (1969) cited Smith's (1965) description of an *E. fulvus* ovary, but Smith did not mention the "typhlosole-type" structure from which ovarian lamellae are suspended that was found in gag gonads in the present study. This structure is also found in *M. phenax*, *M. interstitialis*, *E. adscencionis*, *E. drummondhayi*, *E. flavolimbatus*, and *E. niveatus* (Roumillat, unpubl. data) and may be present in other groupers.

Although Moe (1969) found only 1.43% of red groupers undergoing sexual succession, the percentage of fish with transitional gonads was even lower in the gag (1.25%). These frequencies are much lower than the transitional frequencies of such sympatric species as *Centropristis striata* (14%; Wenner et al. 1986), *Calamus leucosteus* (10-13%; Waltz et al. 1982), *Pagrus pagrus* (10%; Roumillat, unpubl. data), and *Hemanthias vivanus* (9%; Hastings 1981). A rapid rate of sex succession is probably the reason for the low frequency of transitional gonads found. Smith (1965) and Moe (1969) suggested that other groupers have a very quick rate of succession, and Fishelson (1970) and Shapiro (1981) have shown that *Anthias squamipinnis* can change sex within a few weeks.

Despite suggestions that gag transform to males during their 10th or 11th year (McErlean and Smith 1964), it is evident that sexual succession occurs at younger ages. Only seven transitional gag were collected, and of the five that were aged, there was one each in age groups V, VI, VII, VIII, and XI. However, age X was the group in which the sex ratio approximated unity. The age of first maturity for females was lower than the previously speculated fifth or sixth year (McErlean and Smith 1964), and 28% of age III, 51% of age IV, and all older femal gag had mature gonads. Thus, there may be significantly more gag (all females because of protogyny) producing gametes than indicated in the literature, suggesting a greater ability to rebound from intensive overfishing than previously suspected.

Acknowledgments

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AGE AND GROWTH, REPRODUCTIVE CYCLE, AND HISTOCHEMICAL TESTS FOR HEAVY METALS IN HARD CLAMS, *MERCENARIA MERCENARIA*, FROM RARITAN BAY, 1974-75.

Raritan Bay has historically supported an abundant hard clam, *Mercenaria mercenaria* L., resource. It was considered the most important commercial species in the bay with an estimated total value of 34 million dollars in 1963 (Jacobsen and Gharrett 1967). Campbell (1967) reported a total standing crop of 4.8 million bushels of clams for the Bay for the same year (3.4 million bushels in New York waters and 1.4 million bushels off New Jersey). More recent estimates are unavailable.

Raritan Bay waters have historically received various domestic and industrial wastes, some of which have had adverse effects on its shellfish resources and fisheries. Raritan Bay was closed to harvesting of hard clams on 1 May 1961, after an epidemic of human infectious hepatitis was traced to the consumption of raw clams from the bay (Campbell 1967). The closure remains in effect to the present time. Zoellner (1977) reviewed the nationwide water quality problems related to shellfish and included Raritan Bay as one of the case studies in the report.

Bivalves accumulate various biological and chemical contaminants by mechanisms related to their filter-feeding habits and transport across their mucous-covered, semipermeable soft body tissues (Goldberg 1957; George 1982). The accumulation of heavy metals, pesticides, polychlorinated biphenyls (PCB's), oil and dispersants, disease causing bacteria, viruses, fungi, parasites, and toxic phytoplankton have serious public health implications and may also adversely affect bivalve resources. Zoellner (1977) has reviewed natural and manmade conditions affecting bivalve populations, including specific studies of the effects of heavy metals, pesticides, and PCB's. McCormick et al. (1984) reviewed physical and sediment characteristics of Raritan Bay, studies of benthic organisms, plankton, and fish, and impact of pollution from sewage, organic chemicals, and heavy metals.

The present study was undertaken to assess potential impacts of contaminants in Raritan Bay on the spawning potential of hard clams. Monthly samples were collected from three study areas within the bay to obtain measurements of the shells, soft body tissues for observations of general condition, and gonadal tissues for observations of the reproductive cycle. Selected specimens were chosen to determine age and growth, and special tissue samples were collected for histochemical tests of certain metals. Published hydrographic conditions and assessment of pollutants in Raritan Bay are discussed in relation to sample results.

Methods

Campbell (1967) described the distribution of hard clams in Raritan Bay and, based on his findings, sites were chosen for repeated collections. The sites were Ward Point, New Dorp Beach, and Horseshoe Cove (Fig. 1). Each was sampled at about monthly intervals beginning on 21 February 1974 and ending on 7 April 1975. The clams were collected by towing a drag-type, nonhydraulic dredge with a 12-in (30 cm) wide knife from the U.S. National Marine Fisheries Service (NMFS) RV *Rorqual*. Tows were made at each site until 30 or more clams larger than 50 mm in shell length were caught. Special collections were made at Ward Point and New Dorp Beach on 1 November 1978 to obtain tissues for histochem-

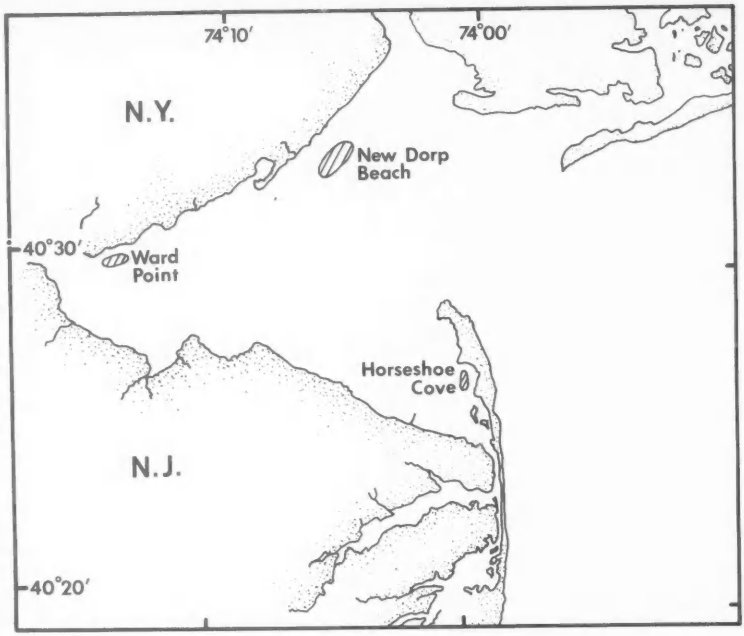

FIGURE 1.—Locations sampled for hard clams, *Mercenaria mercenaria*, in Raritan Bay during 1974 to early 1975 and 1978.

ical tests of some metals, using the same dredge operated from the NMFS RV *Kyma*.

Following sampling operations at each site, the length (longest anterio-posterior dimension), height (deepest dorsoventral dimension from the umbo to ventral shell margin) and width (thickest lateral dimension) of each clam shell was measured to the nearest millimeter with vernier calipers. About 20 clams were then opened and the meat and shell liquor packaged for immediate freezing. Later measurements were made of the drained meat weight, dry meat weight, and percent solids by methods outlined by Ropes (1971a) for other bivalves.

Specimen shells for age and growth observations of hard clams were chosen from Ward Point and New Dorp Beach samples, since clams from these sites exhibited extremes in shell and weight measurements. The selection included five clams in a sample having the smallest mean size, five in a sample having the largest mean size, and those in a sample having a mean size nearly equal to the grand mean for all samples taken at the particular site. The shells were radially sectioned and the cut edge polished to a high luster, as described by Peterson et al. (1983) to facilitate detection of annual growth lines.

Ten additional clams were opened and the soft body tissues were removed for preservation in Bouin's fixative. Methods used for dehydrating, embedding, sectioning, and staining gonadal tissues to prepare slides for microscopic examination of the reproductive cycle were as outlined by Ropes and Stickney (1965) and Ropes (1968). Stages in the development of gonadal tissues were established. The progressive development of sex cells through early to ripe condition and eventual expulsion by spawning activity was a basis for evaluating reproductive viability. Failure to complete all stages of a cycle was considered an indication that the clams were being impacted by environmental conditions.

Specimens were collected for histochemical tests on 1 November 1978 (10 hard clams and 2 oysters from Ward Point and 10 hard clams from New Dorp Beach). The soft body mass of each

specimen was removed on the vessel within an hour of capture. One cm-thick slices were dissected from the central body mass of each specimen and immersed in a vial of fixative appropriate for the histochemical test. Samples were then transported to the NMFS laboratory at Oxford, MD, where slides were prepared for microscopic examination. The following histochemical tests were performed:

1. Inorganic iron. Perl's (1867) reaction, reported in Casselman (1959), to produce ferric ferrocyanide from ferric ions (Fe^{+++}).
2. Arsenites and arsenates. The method of Castel (1936), reported in Pearse (1972), to precipitate the cupric salts of arsenites and arsenates (As^{+++}, As^{++++}).
3. Lead. The method of Cretin (1929), called the chromate method from a reaction with neutral potasssium dichromate, was used, together with the rhodisonate method (Pearse 1972). Both methods are reported in the latter paper.
4. Copper. A method is reported by Uzman (1956) to localize copper by direct treatment of the tissues with rubianic acid. After examining the results of this treatment, the intensification technique to release copper "bound" proteins suggested by Uzman (1956) was also tried.

Results

Hard clams were generally more easily collected at the New Dorp Beach and Horseshoe Cove sites than at Ward Point. Bottom substrata in the dredge with the clams was predominantly a black silty-sand at New Dorp Beach and a relatively clean sand with some shell at Horseshore Cove, but at Ward Point, shell (mostly from oysters) was a major component of the black mud substrata. Live oysters were taken only at Ward Point and their soft body tissues were decidedly green.

Shell and Weight Measurements

Table 1 summarizes the mean, standard deviation, and number of clams for all measurements of clam shell dimensions, weights, and percent solids taken during the study. Values for Ward Point were consistently lower than those for Horseshoe Cove or New Dorp Beach where the values were similar to one another. Student's "t" test revealed no significant difference in measurements between Horseshoe Cove and New Dorp Beach ($P > 0.05$), but a significant difference in all measured parameters was found between clams sampled in these areas and at Ward Point ($P < 0.01$) (Table 2).

Age Observations

For Ward Point, age determinations were made for the 5 smallest (collected 13 January 1975), the 5 largest specimens (collected 19 June 1974), and 8 specimens (collected 24 April 1974) which approximated the overall mean shell length. For New Dorp Beach, similar determinations were made for the 5 smallest (collected 21 February 1974), the 5 largest (collected 22 May 1974), and 13 specimens (collected 1 October 1974) which approximated the overall mean shell length. Some shells in the 24 April 1974 Ward Point and 1 October 1974 New Dorp Beach samples were not prepared for age determination, because severe shell erosion at the umbonal area indicated that early age lines would be incomplete.

Two differences were apparent. Firstly, none of the clams from Ward Point was older than 14 years, whereas clams at New Dorp Beach were as old as 20 years. Secondly, clams at Ward Point on

TABLE 1.—Measurements of the shell and meats of Raritan Bay hard clams, *Mercenaria mercenaria*, collected in 1974 and 1975.

	Sample locations								
	Ward Point			New Dorp Beach			Horseshoe Cove		
Measurements	Mean	SD	No.	Mean	SD	No.	Mean	SD	No.
Shell length (mm)	77.3	9.1	221	88.2	12.7	225	87.0	13.2	230
Shell height (mm)	64.6	9.8	221	74.5	11.0	225	72.6	12.7	230
Shell width (mm)	44.8	5.4	221	50.3	7.5	225	50.6	10.1	230
Shell dry wt (g)	95.0	29.5	201	136.2	48.9	225	138.1	48.7	230
Underwater wt (g)	51.4	15.0	221	74.6	26.7	225	77.6	31.3	230
Drained meat wt (g)	1.3	14.1	201	56.9	18.1	205	55.0	20.9	210
Dry meat wt (g)	5.9	2.1	201	9.0	3.5	205	9.1	4.0	210
Percent solids	14.3	3.2	201	15.8	3.7	205	16.5	3.9	210

TABLE 2.—Results of "*t*" *test comparing measurements of Raritan Bay hard clams, Mercenaria mercenaria*, collected in 1974 and 1975.

Measurements	Sample locations compared		
	Horseshoe Cove and Ward Point	New Dorp Beach and Ward Point	Horseshoe Cove New Dorp Beach
Shell length (mm)	9.0313**	10.3795**	0.9857
Shell height (mm)	7.4520**	10.0069**	1.7005
Shell width (mm)	7.5447**	8.8542**	0.3583
Shell dry wt (g)	10.8928**	10.3523**	0.4143
Underwater wt (g)	11.2380**	11.2120**	1.1330
Drained meat wt (g)	7.7373**	9.6513**	0.9866
Dry meat wt (g)	10.0644**	10.7691**	0.2701
Percent solids	6.2215**	4.3548**	1.8704

** = Highly significant ($P < 0.01$).

average were smaller at each age than those at New Dorp Beach (Fig. 2).

Reproductive Cycle

This part of the study focused on a microscopic examination of the cellular events leading up to an accumulation of sex cells in the gonads and their disappearance during the spawning act. Periodic sampling identified the time and duration of spawning. Cellular structures within the sex cells and alveoli walls were important in determining five stages of gonadal condition, as follows:

Females

Early stage. Alveoli semicontracted, basement membrane thickened, and small oocytes embedded in the alveoli walls.

Late stage. Oocytes more numerous at the basement membrane, some of larger diameter extended into the lumina of alveoli, but attached to

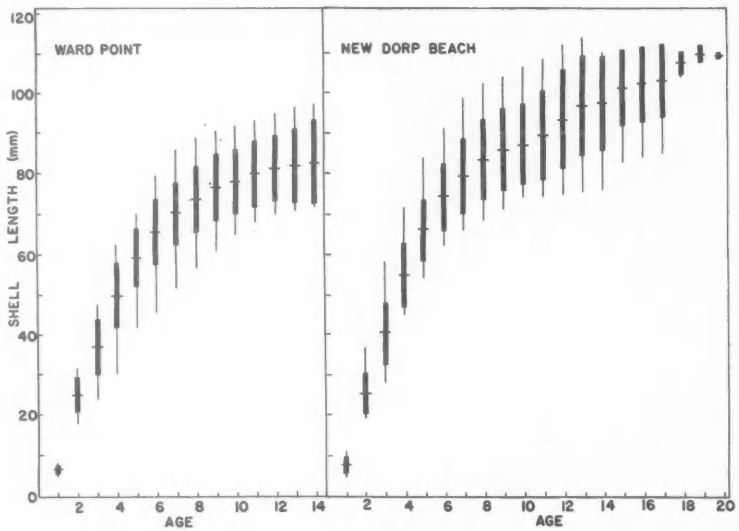

FIGURE 2.—Mean, standard deviation, and range of shell lengths (mm) vs. age (yr) relationships of hard clams, *Mercenaria mercenaria*, at Ward Point and New Dorp Beach, Raritan Bay, 1974-75.

the thickened basement membrane by a stalk. A few of the largest oocytes appear free in the lumina of alveoli. Amphinucleoli prominent in the largest oocytes.

Ripe stage. Numerous large oocytes in the lumina of alveoli. Basement membrane thin, containing only a few developing oocytes. Most oocytes appear free in the lumina of alveoli.

Partially spent stage. Some small oocytes embedded in the basement membrane, with reduced numbers of large oocytes in the alveoli lumina.

Spent stage. A very few of the largest oocytes in some of the alveoli lumina. Basement membrane somewhat thickened and containing small embedded oocytes.

Males

Early stage. Alveoli semicontracted, basement membrane thickened, and follicle cells prominent in the lumina. A few spermatogonia or spermatocytes occur at the periphery of the lumina in most clams, but some with a few spermatozoa scattered in the lumina of some alveoli.

Late stage. Alveoli expanded, basement membrane thin and attached follicular cells less apparent. Primary spermatocytes numerous at the basement membrane, especially during the earliest part of this stage. Secondary spermatocytes and spermatids proliferating into the centers of the lumina. Differentiated spermatozoa arranged in dense radiating bands at the centers of the lumina.

Ripe stage. Lumina of alveoli densely packed with spermatozoa. Fewer spermatocytes and spermatids occurring than in the preceding stage.

Partially spent stage. Few to no spermatocytes or spermatids at the basement membrane. Relatively reduced numbers of spermatozoa in the lumina of alveoli compared to the ripe stage.

Spent stage. Alveoli nearly empty of spermatozoa, but a few near the basement membrane and in the lumina.

For all three sites, gametogenesis progressed from the early to late stages from 21 February to 24 April 1974 (Table 3). Ripening was earliest at Horseshoe Cove, with 10% of the clams in this condition by 22 May and 70% by 19 June. At this latter date, 50% of the Ward Point clams were ripe. Clams at all the sites had ripened by 23 July, and some (20%) at Ward Point and many (70%) at New Dorp Beach were in the partially spent condition, an indication that spawning had begun at these two sites. Spawning was later at Horseshoe Cove, with 67% in the partially spent condition by 21 August. Ripe clams were observed in the sam-

TABLE 3.—Percent occurrence of developmental stages during the reproductive cycle of Raritan Bay hard clams, *Mercenaria mercenaria*, collected in 1974 and 1975.

	1974									1975		
Sample site and gonad condition	2/21	3/28	4/24	5/22	6/19	7/23	8/21	10/1	11/5	1/13	2/6	4/7
Horseshoe Cove												
early	60	70	30	40	10						40	100
late	40	30	70	50	20							
ripe				10	70	100	33	40	30			
part. spent							67	20	60	60		
spent								40	10	40	60	
New Dorp Beach												
early	70	70	70	50							80	90
late	40	20	30	50	100							
ripe						30	30					
part. spent						70	70	50	90	20		
spent		10						50	10	80	20	10
Ward point												
early	40	40	50	40							60	50
late	50	40	50	60	50							20
ripe					50	80	30	30				
part. spent						20	30	50	100			
spent	10	20					40	20		100	40	30

ples from Horseshoe Cove as late as 5 November, but only until 1 October and 21 August at Ward Point and New Dorp Beach, respectively. Partially spent clams were collected from Horseshoe Cove and New Dorp Beach as late as 13 January 1975, but only until 5 November 1974 at Ward Point. The spent and early gametogenic stages identified in clams from all sites by 6 February 1975 indicated that the 1974 reproductive cycle had been completed by all clams and that a new cycle had begun for some. These observations suggest that the spawning period was shortest at Ward Point (5 months) and longest at New Dorp Beach (7 months), with Horseshoe Cove intermediate (6 months).

At all three sites, gametogenesis progressed through morphologically normal stages resulting in the complete spawning of most ripe gametes. Cytolysis of unspent cells was not observed. No hermaphrodites were seen in any of the samples.

The sex ratios of hard clams in the samples were as follows: at Ward Point, 59 males and 60 females; at New Dorp Beach, 56 males and 64 females; and at Horseshoe Cove, 74 males and 45 females. The hypothesis of 1:1 sex ratio was tested by chi-square for all three populations; results indicated a significant ($P < 0.01$) deviation for Horseshoe Cove.

Histochemical Tests for Metals

Histochemical tests were performed on four male and six female hard clams and one male and one female oysters collected at Ward Point; and three male and seven female hard clams collected at New Dorp Beach. The expected histochemical reactions for metals in clam tissues were not observed, i.e., deep Prussian blue for inorganic iron, green granular precipitate for arsenites and arsenates, yellow opaque crystals or scarlet red precipitate by the chromate or rhodizonate methods, respectively for lead, and deep greenish-black precipitate for copper. Thus, the tests for metals in hard clam tissues proved to be negative. Female gonadal tissues tested for arsenites and arsenates from both collecting sites had 1-2 μm diameter granules in the oocyte cytoplasm but the color could not be determined. No similar granules were seen in male tissues. For the two oysters from Ward Point, the deep greenish-black precipitate for copper was evident in connective tissue cells beneath the body wall and palps (a similar reaction was also seen in the epidermal cells of the palps), around the digestive diverticula (Fig. 3), and near the base of cells lining the gills and gut. The connective tissue cells surrounding the male oyster gonadal tubules also tested positive. No similar reaction was seen in the connective tissue cells surrounding the female oyster gonadal tubules, which contained large and apparently normal oocytes. Although not seen in New Dorp Beach hard clam tissues, some gill tissues of hard clams from Ward Point tested for copper showed a slight darkening, but a precipitate was not clearly evident, such as was seen in oysters. The darkening was also absent in underlying connective tissue cells and other tissues. Modification of the technique to intensify the copper reaction was negative for all hard clam and oyster tissues from the two collection sites.

Discussion

Shell dimensions and shell and body weights clearly indicated a smaller size for hard clams at Ward Point than at New Dorp Beach and Horseshoe Cove, which was reflected in the age estimates. Clams at Ward Point were younger (none >14 years) and smaller ($\bar{X}$ = 77 mm; none >97 mm) than clams at New Dorp Beach (none >20 years; $\bar{X}$ = 88 mm; none >113 mm). These are values much lower than the 111 mm mean and maximum length of 144 mm reported for Nantucket Sound hard clams by Ropes and Martin (1960) and recent, almost 60-yr longevity estimate for the species (Ropes pers. obs.).

Determination of the percentage solids for the meats of bivalves is a measure of condition (Engle and Chapman 1953). The following mean values have been reported: 18.4% for soft-shell clams, *Mya arenaria* (Harriman 1954), 17.0% for oysters, *C. virginica* (Engle 1958), 21.4% for surf clams, *Spisula solidissima* (Barker and Merrill 1967), and 18.5% for ocean quahogs, *Arctica islandica*, (Ropes 1971a). These compare favorably with 16.5% and 15.8% for Horseshoe Cove and New Dorp Beach hard clams, respectively (Table 1). The low value of 14.3% for Ward Point hard clams is an indication of poor condition.

Reported age and growth determinations for hard clams suggest that the Ward Point portion of the Raritan Bay population was being adversely affected. Ansell (1968) has extensively reviewed the literature on annual and seasonal growth of hard clams from various investigations in Canada, the United States, and Europe. Length-on-age observations of the growth of hard clams at sites in Florida, North Carolina, New Jersey,

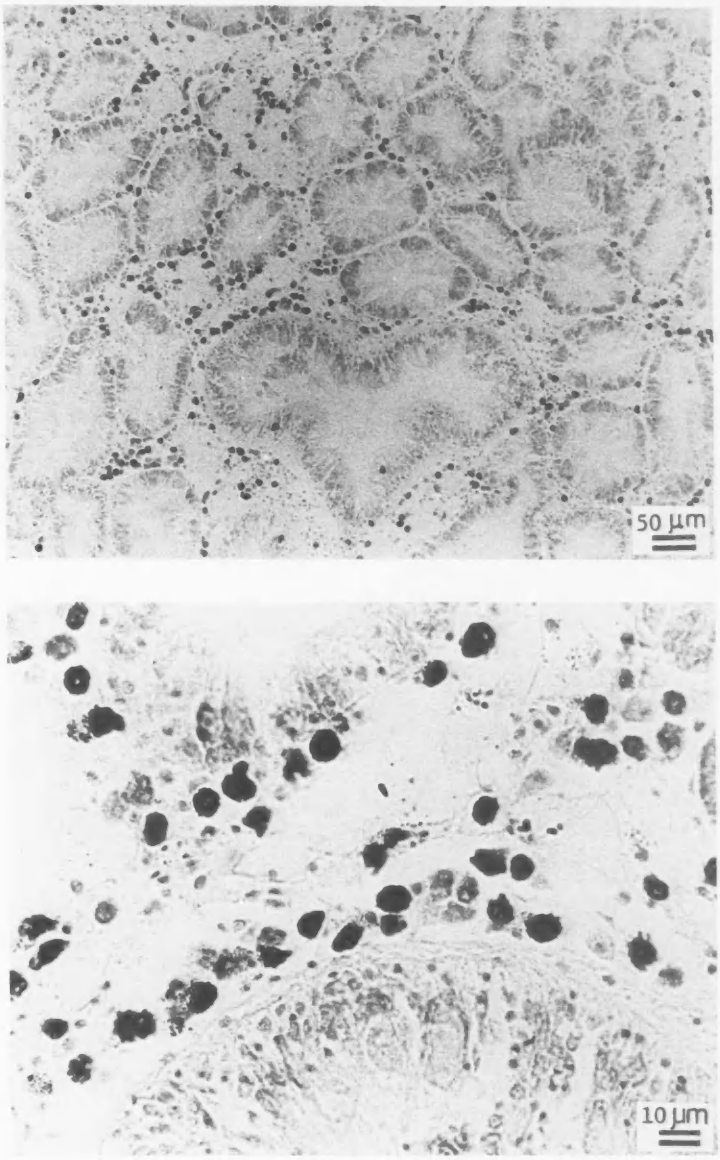

FIGURE 3.—Digestive diverticula of a copper "sick" oyster, *Crassostrea virginica*, from Raritan Bay. Connective tissue cells surrounding the diverticula were greenish black, a positive reaction of copper by the rubianic acid method. A scale of magnification appears in the lower right-hand corner of each photomicrograph.

New York, Massachusetts, Maine, and Canada were compared with the data for the hard clams sampled at the New Dorp Beach and Ward Point, Raritan Bay sites. Growth of Raritan Bay clams was about midway between the fastest (Florida) and the slowest (Canada). At Ward Point, growth to age 4 was about equal to New Jersey growth, but at New Dorp Beach, growth was consistently greater. After age 4, clams at Ward Point grew much slower than New Jersey clams, and even slower than Maine clams after age 5. These observations support the conclusion by Ansell (1968) of extreme local variations in the annual growth of hard clams.

The absence of large, old hard clams in the present samples may be the result of pollution effects, as Jefferies (1972) found for Providence River, RI, hard clams stressed by hydrocarbons. A high C_{15+} hydrocarbon value of 3,672 ppm in sediments at Ward Point was reported by Koons and Thomas (1979). Nevertheless, mortalities (e.g., paired valves containing dead bodies) were not evident at any site.

Food availability is considered an important factor for growth of hard clams by Ansell (1968). Jefferies (1962) considered the nutrient content of Raritan Bay to be rich and the environment capable of supporting dense biotic communities, because of a sluggish circulation pattern. Patten (1962) found that phytoplankton species diversity decreased up bay (towards Ward Point) from the higher values in the Lower Bay. A lower diversity of phytoplankton in the vicinity of Ward Point may have resulted in lower amounts of food organisms being available for the nutritional needs of the clams, and was probably reflected in their slower growth and poor meat condition.

Gonadal development culminated in spawning at three Raritan Bay sample sites. This suggests that the reproductive capacity of hard clams in Raritan Bay was not being affected by pollutants. However, some differences were noted in a comparison of the results based on available information about the time and duration of spawning and larval production at several northwestern Atlantic coast locations. At more northern locations, Belding (1912) and Deevey (1948) in Massachusetts, Landers (1954) in Rhode Island, and Carriker (1959, 1961) in Long Island, NY, and Little Egg Harbor, NJ, observed that spawning was initiated 1 to 2 months earlier than was observed in Raritan Bay during 1974. Similarly, at more southern locations, Keck et al. (1975) in Delaware, Sieling (1956) in Maryland, Ropes (1971b) and Chanley and Andrews (1971) in Virginia, Porter (1967) in North Carolina, and Eversole and Michner (1980) in South Carolina observed that spawning was initiated 1 to almost 3 months earlier. A spawning beginning about three-fourths of a month earlier than the present study was observed by Jefferies (1962) in Raritan Bay, but Loosanoff (1937) in Long Island, NY, observed that spawning began at the same time as in Raritan Bay during 1974. No particular trend in the time of peak spawning was evident in the several studies, except that the peak spawning in 1974 at all Raritan Bay sample sites was later than reported in any of the other studies. Spawning ceased somewhat earlier at more northern locations, and was not as prolonged at more southern locations as was observed in Raritan Bay during 1974.

The project was initiated under the premise that heavy metal pollution in Raritan Bay could be affecting the viability of adult hard clams. Studies indicated that tests for copper and lead should be specifically included, because high concentrations of both have been found in Raritan Bay sediment and water samples (Greig and McGrath 1977; Waldhauer et al. 1978).

The negative results of histochemical tests for heavy metals in Raritan Bay hard clams are not readily explained. Eisler (1981) has listed studies that found 15 heavy metals (including those tested for in the present study) in field collected hard clams. However, heavy metals can occur in several forms (Waldichuk 1979; Fayi and George 1985), suggesting that the histochemical tests may not have been specific for those occurring in Raritan Bay hard clams. Pringle et al. (1968) reported lower levels of copper in field collected hard clams than oysters (*Crassostrea virginica* and *C. gigas*). The positive result for copper in the oysters from Ward Point is probably related to the species greater sensitivity and accumulation of more of the metal in their tissues than hard clams. Copper may have been at a level too low for detection by the histochemical test, although limits for detection of copper or other metals were not given in Pearce (1972).

Hydrographic conditions (not specifically sampled for during the present study) probably influenced the growth and survival of hard clams in Raritan Bay. Based on current flow observed by Jefferies (1962) and Patten (1962), the New Dorp Beach area is influenced principally by water from the Hudson River and the ocean; the Ward Point area is influenced by an eddy formed from

the westward flow of water from the ocean, and flows from the Arthur Kill and Raritan Rivers; the Horseshoe Cove area is affected most strongly by water flowing from the Shrewsbury River.

Ansell (1968) analyzed data from throughout the geographical range of adult hard clams to develop a relationship between temperature and growth rate. Shell growth occurred between temperatures of 9°-31°C and ceased at lower and higher temperatures; the optimum was 20°C. Castagna and Chanley (1973) reported a salinity tolerance range of 12.5-46‰ for survival of adult hard clams, with an optimum of 24-28‰.

The above temperature and salinity limits for adult hard clams were compared with hydrographic results reported by Jefferies (1962). He listed mean surface and bottom water data beginning in summer 1957 to summer 1958 at two locations (Stations 1 and 6) in Raritan Bay near the Ward Point and New Dorp Beach sample sites, respectively. Throughout Raritan Bay no growth of adult clams would be expected during winter due to low bottom temperatures (2.3°-3.0°C); slow growth would occur during the increasing and decreasing temperatures of the spring and fall. Near normal growth probably occurs at New Dorp Beach and Ward Point during the summer when temperature means appeared to be near optimum conditions. Lowest bottom salinities were recorded during the spring at Jefferies' (1962) station number 1 near Ward Point. These values indicate that the minimum salinity tolerance limit for adult hard clams may occasionally be reached in the area. Salinities near the New Dorp Beach area (Jefferies 1962, station 6) were all within the tolerance limits for adult hard clams.

Jefferies (1962) reported dissolved oxygen measurements and found relatively low concentrations in the water near Ward Point in both summer periods. Slightly higher values occurred in the fall of 1957 and following spring near Ward Point, but the confidence intervals were greater than for any other period, indicating more variable conditions. Dissolved oxygen levels near New Dorp Beach were consistently higher than near Ward Point.

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ERRATA

Fishery Bulletin Vol. 85, No. 1

Utter, Fred, David Tell, George Milner, and Donald McIsaac, "Genetic estimates of stock compositions of 1983 chinook salmon, *Oncorhynchus tshawytscha*, harvests off the Washington coast and the Columbia River," p. 13–23.

Page 16, Table 1, Stock group, correct to read as follows:

California	6
Puget Sound and British Columbia	4

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